
BRITAIN'S GREEN MANTLE

by A. G. Tansley

INTRODUCTION TO PLANT ECOLOGY

THE NEW PSYCHOLOGY
AND ITS RELATION TO LIFE

(George Allen & Unwin Ltd)

THE BRITISH ISLANDS AND THEIR
VEGETATION

OUR HERITAGE OF WILD NATURE

(Cambridge University Press)

TWO WIND-CUT OAKS

N. T. Porter

Moderately wind-cut oak near the top of Inkpen Beacon (1000 ft.) in Berkshire, the highest point in the neighbourhood. The tree inclines to the north-east, away from the prevailing south-west winds which have uninterrupted access.

N. T. Porter

Much more severely wind-cut oak near the east coast. The trunk, thickly covered with short twigs, is sharply bent towards the west, away from the violent east winds.

Frontispiece

A. G. TANSLEY

BRITAIN'S GREEN MANTLE

PAST, PRESENT AND FUTURE

With 144 photographs

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PREFACE

THE title of this book is unashamedly copied from *Earth's Green Mantle*, published by my old pupil, Professor Sydney Mangham, in 1939. The face of Britain, in spite of the enormous growth of building, is still mainly covered with a green mantle of vegetation, a large proportion of which is grassland, green even in winter.

It is, however, with only part of the whole that this book is directly concerned, that is to say the natural and what we call the "semi-natural" vegetation of the country. The farm crops form a topic which would have to be treated quite differently and cannot be conveniently dealt with in the same work, though a general account of them, past, present, and future, is much needed and would be a subject of fascinating interest. The natural vegetation of the country, which is determined by climate and soil alone, with the semi-natural vegetation, which still consists of native plants but has been modified by man's activity though not replaced by planted crops, evidently has a primary interest of its own and forms the basis of that precious "heritage of wild nature" which was briefly described in my little book [1] published in 1945.

The present book is intended for all who want to know more about our native vegetation, what it consists of, and how it came to be what it is, but have no time or no inclination for specialised study. It is written so as to be easily intelligible and the few technical terms used are clearly explained. I have included only so much of the material contained in my large work [2] as I thought might be of interest to all who love our wilder countrysides; but the aim has been to furnish a good deal of solid information. Pages 37 to 40 in Chapter III, dealing with the structure of soil, and some passages in Chapter V are perhaps a little too technical for the general style of the book, but they may be useful to some readers.

We have to recognise that the whole of our natural and

[1] *Our Heritage of Wild Nature: a Plea for Organised Nature Conservation.* Cambridge University Press, 1945.

[2] *The British Islands and their Vegetation.* Cambridge University Press, 1939.

semi-natural vegetation is based on a number of "plant communities," each determined by the particular conditions of the places in which it lives—heath, moor, fen, bog, salt marsh, hill grassland, as well as the different kinds of woodland which in our climate naturally come wherever trees can successfully establish themselves if they are allowed to do so and are given time. These natural communities may be more or less altered without being destroyed by human activity, and then appear in modified forms, as when a wood is coppiced, a chalk down grazed, or a fen mowed. Sometimes man creates new habitats for plants, such as railway-banks, hedge-banks, road-sides, or stone walls, which are then colonised by a mixture of plants from various natural communities that are able to find and maintain a footing in such places. The plants living in these artificial habitats have up to now received very little systematic study, and I have only been able to refer to them incidentally in the course of the book, though it is this kind of vegetation which often first meets the eye of the traveller or wanderer. Still, it is the natural plant communities and their immediate derivatives which form the basis of the whole, and without a knowledge of them we cannot understand the make-up and distribution of any native vegetation.

All the plants mentioned are referred to by their English names where these exist and are in at all common use, the scientific names being usually added in brackets. It should be realised that a large number of our native species have no English names because they have not attracted the attention of any but botanists. English names invented *ad hoc* have been avoided, since they have no general currency and no particular value. *Local* names are often interesting and attractive, but mention of such of them as one happens to know would scarcely be in place in a general work.

In order to avoid long and wearisome lists of species only those which are most characteristic of the different communities are mentioned in the descriptions.

A. G. T.

GRANTCHESTER, CAMBRIDGE.
July 1947.

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THE PLANT COVERING AND ITS CHANGES

Prehistory

FIRST of all let us glance for a moment at the existing plant covering of England, and of Great Britain, and then compare it with the natural vegetation of prehistorical and early historical times. We can properly speak of "the existing plant covering," for though the growth of towns and cities has been enormous and it is naturally these which bulk most largly in the perspective of those who live in them, yet "built-up areas" still occupy not much more than an eighth (about 13 per cent.) of the whole surface of England, though they contain the vast majority of the population. The rest of the country is covered with vegetation of various kinds. Before the Second World War over half of the whole area was grassland of one kind or another, less than a quarter under arable crops, about a twentieth woodland, and perhaps rather more than that heath, moorland, and bog.

The grassland was mainly so-called "permanent grass," that is to say enclosed grass fields maintained for pasture and some of it cut for hay. A small fraction was under "temporary grass," known as "ley," alternating with arable crops. A landscape of grass fields enclosed by hedges, or in the north by stone walls, was much the commonest sight from the windows of a train, except in parts of the east and south where arable land predominated, and in the northern hill and mountain regions where the railway lines crossed wide stretches of moorland.

The vigorous ploughing campaign during the war has altered this picture considerably. In the total "farm area" of England and Wales the percentage of tillage increased from 28 in 1939 to 48 in 1944, of leys from 8 to 12 per cent., while the permanent grass decreased from 64 per cent. in 1939 to 40 per cent. in 1944. In the midland

counties, which were almost all in permanent grass, this change has been greatest. Thus in Leicestershire—a county famous for fattening bullocks on its excellent pastures—the tillage area increased from 58 to 191 thousand acres, in Warwickshire from 73 to 226 thousand. In the west the change has been equally marked. In Somerset the tillage increased from 96 to 254 thousand acres, and in Carmarthenshire from 25 to 111 thousand. This increase in our arable land, which has brought new life to much of the countryside, we may expect to see largely, though not wholly, maintained in the years to come.

But perhaps a fifth of the English and Welsh grassland was unenclosed "rough grazing," mostly traditional sheep pasture, as on the chalk downs of the south and the hillsides of the north and west. In Wales there was much more rough hill grazing and much less arable land; in Scotland, with its Highlands and "Southern Uplands" (separated by the low-lying arable and industrial "central valley") occupying most of the country, more rough grazing still and very much less enclosed grassland, which was here less than a sixth of the whole grazing area as compared with four-fifths in England. In the Highlands, too, there is, of course, a great deal more bog and bare rock and moorland which is of little use for grazing, though sheep and cattle are allowed to wander over the more accessible moors and pick up what they can find. Most of this land, however, was kept for sport, either as "grouse moor" or "deer forest" in which the great herds of wild red deer were preserved for stalking. Both these uses brought in much bigger rents than could be obtained from letting as sheep farms.

The outstanding feature of this picture is the predominantly pastoral character of the whole country. And this is still true in spite of the changes brought about by the war. Sheep rearing has been a leading occupation in Britain ever since Neolithic times 4000 years ago. In the Middle Ages, and again under the Tudors at the beginning of the Modern period, the area devoted to sheep increased enormously with the rise of the great export trade in wool and cloth. The extension of grassland for sheep pasture was at the expense of the forests which had previously covered most

of the country. Forest was felled in the first place to obtain timber for construction, wood for tools and utensils, and firewood, and then to make room for sheep and cattle. The British climate with its cool summers, well-distributed rainfall, and almost constantly moist air is particularly well suited to the growth of grass, and even where forest was not cleared, but cattle were grazed within it, grassland eventually came in its place as the trees died and seedlings which would have regenerated the forest were destroyed by grazing and trampling.

Let us now look back ten thousand years or so and see what the vegetation was like at the beginning of post-glacial times, i.e. after the repressing influence of the Great Ice Age was removed from the plant life of the country. We can do this with some confidence because during the last twenty-five years we have learned vastly more than we knew before about the history of the vegetation which occupied the country after the ice sheets had disappeared. Previously we had only fragmentary evidence, obtained from peat deposits, of the kinds of wood, seeds, and dry fruits, such as fir-cones, acorns, and hazel-nuts, that were found embedded and preserved in the peat. We knew that there had been periods of wet climate between then and now, during which bog mosses and other bog plants [1] had flourished and formed peat in many areas. We knew, from their wood preserved in the peat, that birch and pine had grown in what are now treeless and peat-covered regions; and that pine and oak had flourished at many places round the coast, forming the so-called "submerged forests" whose remains are found between and below tide-marks, giving evidence of considerable subsidence of the land (or raising of the mean sea level). But from this piecemeal evidence we could not reconstruct anything like a continuous history of the vegetation. It was due to the work of the Swedish naturalist Lagerheim that the method

[1] In ordinary language the word *bog* is commonly applied to any area of saturated soil into which the foot sinks, but here it is restricted to wet peat soil, acid in reaction and inhabited by the characteristic bog mosses (*Sphagnum*) and certain flowering plants such as cotton-grass, sundew, bog asphodel, etc., whose partial and arrested decay forms the peat on which successive generations of the bog plants live. See Chapter XI.

of "pollen analysis" of peat was inaugurated, and after 1920 applied to the peat deposits of the British Isles. This method has enormously advanced our knowledge of prehistoric vegetation.

Vertical bores are made through the peat, which is often many feet in thickness, and samples are taken at different depths from the "core" brought up by the borer. After special treatment these samples are examined under the microscope, and pollen grains of various plants, often in great numbers, together with the spores of ferns, are found to have been preserved in the peat. The pollen grains of different plants have characteristic and easily recognisable shapes, and owing to their resistant ("cutinised") skins many of them are preserved in peat for many thousands of years without suffering much change of form. These grains, blown about by the wind, were caught in the surface of the living bog or fen,[1] and as this grew up they became embedded in the peat formed by the continuous growth and partial decay of the bog or fen plants. Thus a series of samples from the surface downwards gives a record of the grains caught at successively earlier periods.

The pollen found in the peat is not derived exclusively, or even mainly, from the flowering plants actually growing in the fen or bog. Owing to the ease with which many kinds of pollen are carried long distances by the wind, the grains falling on the surface of the bog or fen come very largely from the surrounding country, and thus those found in a given sample provide an index of the composition of the vegetation of the whole region at a particular time. Various considerations enable an estimate to be formed of the proportion of the pollen coming from plants growing in, or on the edge of, the peat area, and of that coming from the surrounding country. In the great majority of cases where the climate is suitable for tree growth, as in Britain, the pollen that has been carried a comparatively long distance by the wind and has settled on the bog surface is mainly tree pollen, and thus furnishes a record of the composition of the forests that covered the country at any given time. Tree pollen, of course, has a much better

[1] A *fen* is a peat area, neutral or alkaline in reaction, bearing quite a different vegetation from a bog. See Chapter XIV.

chance than the pollen of low-growing plants of being carried by the wind for a considerable distance, because it is discharged at some height above the ground. Also most tree pollen is well suited for wind carriage.

Furthermore, it is possible to *date*, approximately, the age of any given sample of pollen occurring at a particular level in the peat. The time scale used was calculated by the Swedish geologist De Geer from the number of alternating coarse and fine layers of silt deposited in certain Swedish lakes. Each pair of these layers ("varves") represents the deposition of silt in a single year, the coarse layer being the deposit in winter, when the streams flowing into the lake are swollen and can carry coarse material, and the fine layer the summer deposit. By counting the number of varves in different lakes at different latitudes in Sweden De Geer was able to ascertain the number of years that had elapsed since the retreat of the ice from the corresponding latitude, and thus to construct a time scale for the whole post-glacial period. This time scale or "geochronology" can be correlated with the nature of the peat, with the records of the presence and frequency of various trees revealed by pollen analysis, and with the archaeological data obtained from the human implements and other remains (which are often found embedded in peat or silt) left by the different races of men that successively occupied the country. The succession of different types of forest revealed by pollen analysis corresponds in a general way over wide areas of Europe, though with more or less important differences of detail; and from these data, and from the nature of the peat at various levels, periods of different climate can often be confidently inferred.

These various lines of investigation—geological, climatological, botanical, and archaeological—have been extended through the greater part of Europe and together they give strikingly concordant results. Thus we can now present a good general outline of post-glacial history, though much further research is needed before all the details can be filled in and doubtful points satisfactorily cleared up. In what follows the post-glacial history of the vegetation in this country is outlined in general terms, so as to avoid encumbering the story with specific references to the now

copious evidence on which it is based. With the active research which is now going on the successive pictures of the vegetation that have been constructed are always liable to alteration in some details, but the main story is securely established.

When the ice sheets of the last glacial phase gradually retreated northwards, finally disappearing from the lowlands somewhere about 10,000 to 8000 B.C., they left behind great lakes and meres and much waterlogged ground in the low-lying country. The rivers and streams were larger and the land relief greater on the whole than it is now, the chalk downs, for example, being higher and more extensive because they had not then been worn down and worn back so far by the solvent action of rain. Our southern chalk was continuous with the French chalk across what is now the eastern part of the English Channel and the Straits of Dover, and the flat lands of eastern England were continuous with Jutland and the Netherlands across the area now occupied by the southern part of the North Sea. This wide plain extended for more than 200 miles from the present Netherlands coast, at least as far north as the 50-metre (about 160 feet) depth contour line of the existing North Sea—a line which runs from the Yorkshire coast north-eastwards into the Skager Rak north of Jutland. From the sea bottom south of this line "moorlog" has been dredged up in many places. This peaty substance contains pollen grains and other remains of a vegetation which shows that the moorlog was formed on land during what is known as the *Pre-Boreal period*, not very long after the close of the last phase of the Ice Age. Through this plain the Rhine flowed northwards and the Thames was one of its tributaries. Britain was in fact a north-western peninsula projecting from the European continent.

As the temperature rose in the Pre-Boreal period (about 8000 B.C.), which followed the arctic conditions of the end of the last glacial phase, trees began to spread, replacing the tundra vegetation of dwarf shrubs, mosses, and lichens, such as is now found in Lappland, Northern Russia, and Northern Siberia. Many of the trees doubtless came across the wide land bridge which joined Britain to the continent,

but it is quite likely that some at least of the kinds represented were already in the country. In the last glacial phase southern and eastern England and the midlands were not covered by ice, which was confined to the north and west, and several kinds of tree may very well have survived through this phase from the preceding warmer "inter-glacial period" (between the last but one and the last glacial phase) in which we know that a temperate flora flourished. In the increasing warmth of the Pre-Boreal period any such surviving kinds of tree would naturally spread. Willows settled round the meres and on the wet ground of the lowlands, while birches, and a little later pines, spread over the uplands. There were also present, in some places, hazel, oak, elm, and alder, in smaller quantity.

The climate now became dry and warm, the mean July temperatures being perhaps 2° C. (3·6° F.) above those we have to-day.[1] These conditions are believed to have lasted about 2000 years (7500 to 5500 B.C.) during what is called the *Boreal period*. Pine forest occupied most of England and penetrated to Ireland and northern Scotland, though in the north pine was never so common as birch. Hazel also increased enormously, perhaps forming great areas of scrub in front of the advancing forest. England was at that time inhabited by peoples known as Mesolithic, who made distinctive types of flint implements. Like their Palaeolithic predecessors, who seem to have disappeared about the end of the last glacial phase, they were hunters, not agriculturists, and would have little effect on the vegetation. In parts of England elm, and later oak, increased at the expense of pine during this period, so that extensive forests of broad-leaved trees must have been established locally as the Boreal period progressed. During the whole of this time the land was sinking and the sea gradually invading the low-lying land bridge to the continent. By the end of the Boreal the surface of eastern England was at least 100 feet lower than at the beginning.

The climate while remaining warm now became much

[1] This estimate is made from the extent of the northward range in Scandinavia of certain warmth-loving plants during the Boreal period, a range which was markedly greater than it is to-day.

wetter, the surface of the land continuing to sink relatively to sea level, in eastern England at least, till Britain was completely isolated from the continent. The expansion of deciduous forest dominated by oak that occurred in Boreal times continued until oak forest became the prevalent vegetation over most of the island, and it has remained the characteristic British woodland ever since. The beginning of this moist, so-called *Atlantic period*, which lasted for approximately 3000 years, i.e. until about 2500 B.C., was marked by the great increase of alder, which must have been extremely abundant in the oak forest, while pine correspondingly diminished, except in Scotland. Elm remained a characteristic tree (probably wych elm, and possibly other species in the south and east), and lime (now rare and local as a native tree) was abundant at certain places, especially in eastern England, throughout the period. Hazel was probably the dominant shrub of the underwood, as it still is. The long-continued dry Boreal climate had led to invasion of the eastern fens by trees, especially pines. With the wet Atlantic conditions the fens were now invaded by bog moss (*Sphagnum*), which again destroyed these marginal forest growths.

In the later part of the Atlantic period Mesolithic cultures were superseded by Neolithic, marked by an improved type of flint implement. The Neolithic peoples were the first inhabitants of the country to practise agriculture and to keep flocks and herds, and during the succeeding 4000 years up to the present day cultivators and pastoralists have increasingly and profoundly modified the vegetation, though they could not change its basic natural character, which is determined by climate. The Neolithic peoples settled on the drier areas, mainly on chalk and oolite uplands such as the Yorkshire Wolds, the Cotswolds, and Salisbury Plain, in smaller numbers on the South Downs and on the Lincolnshire Wolds, and also on the Mountain Limestone of the Mendips and the Southern Pennines. Though there is no direct evidence, it is very probable that these areas were mainly forest-covered while the warm wet Atlantic climate persisted, but when it became drier, as it apparently did before the end of the third millennium B.C., the trees on these thin porous soils would inevitably suffer.

A primitive people keeping sheep and growing cereals would first of all settle in the most open places, for example the windswept summits and ridges of the downs where there was grass for the stock and woody vegetation was absent or sparse, so that any there was could be easily cleared. If the climate became drier and the trees on the slopes also began to suffer, grazing could be extended, and the more it was extended the farther the forest margin would be driven back. Thus the decrease of moisture and the presence of man and his grazing animals would alike tend to push back the forest and extend the grassland area.

The transition from the Atlantic to the succeeding climatic period, known on the continent as the *Sub-Boreal,* is not well marked in Britain. We know that part of the latter period was relatively dry, as is shown by the fresh spreading of pine [1] at this time on the East Anglian fens and also on the drying peat of Scottish and Irish bogs; but the climatic history of the later Atlantic and much of the Sub-Boreal is still obscure and the evidence is to some extent conflicting.

Soon after 2000 B.C. the use of metals, originating in the Near East at least 2000 years earlier, was introduced into Britain by the peoples who established the "Bronze Age" cultures which lasted here for nearly 1500 years. The Bronze Age peoples were more numerous and spread more widely over the country than their Neolithic predecessors. In the south they do not appear to have lived on the chalk downs themselves, for though Bronze Age tumuli (barrows) are very numerous on the chalk there is little evidence of actual dwellings, in striking contrast to the Neolithic remains. It is widely believed that increasing dryness of the climate led to a deficiency of water which made the downs themselves uninhabitable. This view accords well with the suggestion we have made that during Neolithic times increasing pasturage and increasing drought had led to extension of the originally small grassland areas at the expense of forest, so that in the Bronze Age the downs had become mainly grassland used for traffic, grazing and burial

[1] The layer of birch stumps separating the underlying Atlantic from the overlying Sub-Boreal peat is shown in Photograph 1. Above is seen the dark spongy Sub-Atlantic peat, the top of which is destroyed.

sites but not for habitation. This picture is also supported by the existence of a well-marked layer of old turf which seals the Neolithic pits and the remains of Neolithic camps, and on which the Bronze Age barrows were constructed.

In the lowland valleys, on the plains, and probably on the more extensive chalk plateaux where these are covered by clay or loam more retentive of water, as on the Chiltern Hills, the Hampshire Uplands, and the North Downs, the oak forest remained. The lime tree, however, almost disappeared, and two other trees, beech and hornbeam, began to spread, though their detailed history and the limits of their extension are not yet known.

About the middle of the first millennium B.C. the climate deteriorated, becoming wet and much cooler. The oak forest still maintained itself, but pine receded, and peat was again formed actively in the bogs and fens. The beginning of this *Sub-Atlantic period* was marked by the invasion and settlement of peoples who used iron for their tools and weapons, and corresponds, in Britain, with what is called the "Iron Age." [1]

The establishment of the Sub-Atlantic climate, which is essentially the *type* of climate we have in England now, gives us a datum or starting-point from which to consider the changes in the vegetation that have taken place as the result of human activity during historical times. Doubtless there have been minor climatic fluctuations during the last 2000 years: there is some evidence that ameliorations occurred in Roman times, again about A.D. 1000 and perhaps also in more recent centuries. But none of these has been sufficient to change the main features of the vegetation, though they may have made the cultivation of warmth-loving plants such as the grape vine more successful than it would be to-day.

We may picture the natural vegetation of the country at the time of the Roman occupation, i.e. in the later Iron Age, somewhat as follows. While there was fairly extensive cultivation on the chalk and also on the loam soils of the south-east, most of the English lowlands, for example

[1] In Photograph 2 the sharp limit between Sub-Boreal and Sub-Atlantic peat is probably marked by the logs laid down on the bog to form a "corduroy road."

W. M. Rankin

PHOT. 1. Section of peat in North Lancashire. Birch stumps underlain by Atlantic and overlain by Sub-Boreal peat marking a drier climatic period. Above is dark spongy Sub-Atlantic peat.

Elizabeth Cowles

PHOT. 2. "Corduroy" road made of logs against whose cut ends the trowel is held. This probably marks the top of Sub-Boreal peats.

Face p. 10

the Weald and the Midland Plain, were covered with oak forest, mainly uninhabited and harbouring wolf, lynx, and bear, besides numerous deer. Oak forest also occupied the sides of the valleys in the hill and mountain regions of the west and north, giving place to pine and birch woods at higher levels and on the poorer and more sandy soils. In the extreme north of Scotland there was little or no oak even at low altitudes, though oak forest filled the bottoms and lined the lower slopes of the larger glens in the Central Highlands. In the limestone regions, for example on the Mountain Limestone of the Northern and Southern Pennines, ashwood, the remains of which may still be seen in the Derbyshire dales (Phot. 37, p. 116), probably covered the sides of the valleys.

In the Bronze Age the upper forest limits in the north were substantially higher than at present, reaching at least 3000 feet in parts of the Highlands, as compared with about 2000 feet, which is the highest altitude on protected slopes occasionally attained by trees to-day. The depression of the upper limit of forest was probably due primarily to the bleak sub-Atlantic climate, but the general deforestation, the results of which we see to-day, of the slopes of most of the northern hills down to much lower levels has been the result of grazing.

On the rounded tops of some of the northern hills where the ground was well drained, both on limestones and on other rocks, at about 2000 feet, there was grassland in the Bronze Age which probably had a history somewhat similar to that of the southern chalk downs in Neolithic times. Naturally destitute of trees because of their extreme exposure to strong winds, they were used for grazing by prehistoric peoples, largely in the Bronze Age, but unlike the downs they were never tilled because crops cannot be raised at that altitude. Such high-level grazing grounds are known, for example, in the Cumbrian Lake District.

Throughout the lowlands waterlogged areas were studded with many shallow meres surrounded by marsh or by fen [1] partly covered with willow and alderwood. Many such

[1] The word *marsh* is used for a waterlogged area with mineral soil, *fen* for a waterlogged area with abundant lime in solution and a peat soil. See p. 220.

small fens are still found in the flat bottoms of valleys where the water drains from calcareous rocks, but the most extensive (now drained and cultivated) occupy the sites of old estuaries from which the sea retreated and the salt was washed out by rain. Towards the sea these estuarine fens pass into salt marsh where the tides still have access, as in the East Anglian Fenland (the Wash) and the Somerset Levels (estuary of the Parrett). When the alkaline fen peat, fed by lime-containing ground water, has grown up above the winter water level, bog plants, largely bog moss (*Sphagnum*), begin to replace the fen vegetation and form bog- or moss-peat [1] which receives its water directly from the abundant rainfall of a wet climate and is kept moist by the damp air. Thus the acids developed by the plants are no longer neutralised by the calcareous ground water and bog supersedes fen. Such bogs are called *raised bogs*, because their surface is slightly convex and is above the level of the surrounding fen. Many still remain in the central plain of Ireland, though in England most have been drained and destroyed.

Bogs forming the same kind of peat and inhabited by many of the same plants occupy wide undrained areas not much above sea level in the wettest climates of all, i.e. in western Scotland and western Ireland, and these are called *blanket bogs* because they cover the country like a blanket. Blanket bogs also spread over high-lying plateaux where the drainage is poor and the rainfall heavy, as on Dartmoor, the Pennine plateaux, and in the Scottish Highlands. All these features of still existing fen and bog vegetation probably took shape at the beginning of the Sub-Atlantic period.

The peoples of the Iron Age, with contemporary Bronze Age survivors in the north and west, having to exist in a cool wet climate, naturally chose the driest sites for their dwellings and cultivation. The chalk uplands of the south and east were used by even more numerous populations than in the Bronze Age, and here no doubt were the largest areas of pastoral grassland as well as ploughland; but there is evidence of widespread occupation of the drier soils in other parts of Britain. The Iron Age people con-

[1] See Chapter XI.

structed many of the hill forts and camps the remains of which are still conspicuous both on the chalk and in other parts of the country.

The later Iron Age invaders (Celts) were Belgic people from the neighbouring continent who came in the first century B.C., not very long before the first Roman invasion under Julius Caesar. They not only occupied the southern chalk but also settled largely on adjacent loam soils in what is now Essex, Hertfordshire, and East Anglia, the Thames valley and the Kentish and Sussex coastal plains. They founded, in fact, quite powerful small kingdoms, some of which put up a stout resistance to the Romans, while others became their allies. The Belgae practised an improved type of agriculture, probably using wheeled ploughs and producing a surplus of corn and cattle which they exported to the continent. Caesar found Kent densely inhabited for those times and easily obtained enough corn and cattle for his troops.

On Salisbury Plain and on the downs of Berkshire, Wiltshire, Dorset, and Sussex the so-called "Celtic fields" whose nature and extent were first made plain by O. G. S. Crawford (largely by means of photographic survey from the air) are believed to have been cultivated throughout the centuries of Roman occupation. "In Romano-British times [writes Crawford] practically the whole of Salisbury Plain, Cranborne Chase, and the adjacent Dorset uplands were under the plough." These Celtic fields are rectangular in shape and are bounded by "lynchets"—low banks thrown up by the plough—which still remain in many places on the southern chalk, often perfectly preserved, though the whole is now covered with grass.

CHAPTER II

THE PLANT COVERING AND ITS CHANGES

The Historical Period

THE Roman conquest was responsible for a good deal of forest destruction and the long occupation must have led to considerable extension of agriculture, but it seems to have had comparatively little effect on the vegetation of the country at large. The Romans were great town-builders and road-makers, but they brought about no fundamental changes in British rural economy. The great forest areas in the south, for instance of the Weald, of south-west Essex and of the Midland Plain still remained, and much woodland was also maintained between the areas occupied by the Roman villa farms and the British hamlets. Many of the larger forests were probably scarcely penetrated except for hunting, though the Weald was partly exploited for charcoal used in smelting the iron obtained from its ferruginous sands.

It was not till the coming of the Saxons in the fifth century of our era that clearance of valley woods for agriculture was greatly extended and the Celtic cultivation of the chalk plateaux and summits practically ceased. Most of the Celtic inhabitants were exterminated or driven into the west and their cultivated fields left derelict. The Saxons were lowland cultivators and began to clear the forest from the valleys and low-lying plains. As Wooldridge has shown, they occupied at first the lighter loam soils of south-eastern England which had already been exploited by their Belgic predecessors, since these were both easier to till and more immediately fertile than the heavy clays, which were, besides, often water-logged in the winter. The Saxon cultivation afterwards extended to the claylands, but considerable areas of these remained for another thousand years covered with thick forest. The abandoned "Celtic fields" on the downs

are now largely typical chalk pasture, but many of those on the chalk plateaux which were covered by a layer of clay or loam over the chalk were invaded by shrubs and trees—largely oak and to some extent beech—and in some of the woodlands thus naturally established and still extant the boundaries of old cultivation can still be traced.

Thus it was the Saxons who began the clearance of lowland forest which ultimately turned England from a mainly forest-covered into a largely agricultural but predominantly pastoral country. The Danish and Norse invaders who alienated practically the whole of the east and north from Saxon control in the ninth and tenth centuries probably had little effect on the natural vegetation, since they settled mainly on land previously occupied. It was otherwise with the Norman conquest of 1066, and the changes brought about by Norman domination were far-reaching.

In the first place, the Normans systematically devastated large portions of many counties in order to overawe the Saxon population, destroying crops, farm animals, and houses; and land so treated must have been largely invaded by wild vegetation before it was reclaimed for agriculture in after years. Secondly the Norman kings formed "Royal Forests" for hunting by placing certain areas under "Forest Law" and forbidding as far as possible cultivation within their limits. The areas so reserved were not necessarily covered with trees, but included heaths and moorlands such as parts of the New Forest in Hampshire, Dartmoor Forest in Devon, and the Peak Forest in Derbyshire, but all the Royal Forests were probably based on tracts of natural vegetation and many of them were old tree-covered lands. The actual extent of the Royal Forests, which seems to have reached its maximum in the middle of the twelfth century, is not accurately known, but some authorities place it as high as one-third of the whole country and it is known that even entire counties were placed under Forest Law. Cultivation within the forest boundaries was discouraged by fines levied in the Forest Courts, but a certain amount must have been carried on or the country could not have been fed.

The net result of the devastation of agricultural land and

the formation of Royal Forests was clearly to check and even to reverse, for at least a century, the progressive conversion of wild into agricultural land. But in the later part of the twelfth century it became clear that "afforestation" had gone too far and the reverse process, "disafforestation" of the Royal Forests, began; thereafter the extension of pasturage and agriculture proceeded throughout the rest of the Middle Ages.

Side by side with "assarting," i.e. the clearance of forest land for tillage, went the grazing of cattle, as well as pigs, in the forest itself. It is believed that the feeding of swine in oak or beech forest actually assisted regeneration of woodland through the pigs stamping a certain proportion of acorns or beechnuts into the soil, where they are more likely to germinate successfully than when they lie on the surface. Also the destruction by the pigs of small vermin such as slugs, snails, mice, and voles, which to-day make regeneration impossible by destroying the nuts and seedling trees, would work in the same direction. But the extensive pasturing of *cattle* through forest always leads to the disappearance of the woodland plants, consolidation of the soil by trampling, and the introduction of grass vegetation —conditions which make the germination and establishment of tree seedlings more difficult, apart from their destruction by browsing, and thus lead to the disappearance of the forest as the old trees die.

From Anglo-Saxon times throughout the Middle Ages a large part of English arable cultivation, extending over much, though not the whole, of the country, was in the form of "open fields," cultivated in common, belonging to the village communities, and remains of this system lasted into the nineteenth century. The village names of these common fields—"Barton Field," "Madingley Field," "Comberton Field," etc., may still be seen on the Ordnance Maps of Cambridgeshire published in 1886. The people also had extensive rights of pasture and collection of dead wood in the forest "wastes." The grazing of stock in these wastes prevented, as we have seen, the regeneration of woodland and led to its degradation into rough grassland or heath interspersed with bushes—largely thorny shrubs such as hawthorn, blackthorn, and gorse, which can

resist the attacks of grazing animals and are still characteristic of many old "commons." The common land, both "field" and "waste," was, however, increasingly enclosed in later centuries; and this process culminated in the Enclosure Acts of the late eighteenth and early nineteenth centuries by which the greater part of the common rights were finally alienated from the people.

When "subsistence farming" was largely replaced during the Middle Ages by farming for profit the proportions of arable and pasture fluctuated with the prices of corn on the one hand and wool and cloth on the other, all of which were exported in quantity at various times. Apart from agriculture the making of textiles was the great English mediaeval industry, and in its most prosperous period enormous flocks of sheep were maintained for their wool. The importance of the grazing industry led to constant increase of grassland, though agriculture proper, often very prosperous, maintained itself side by side with sheep and cattle raising. With the marked and progressive decline of agriculture in the later nineteenth century and the beginning of the twentieth, more and more land was converted to "permanent grass" until before the late war more than half the total area of England and Wales was occupied by grass fields. In the north, where the climate is less favourable to agriculture proper, so that the rural population was almost entirely pastoral, the sheep were grazed on the hillsides, originally covered with oak forest on the siliceous rocks and ash forest on the limestones. The lower slopes on the sides of the valleys, and in limestone country also the plateaux (Phot. 37, p. 116), were largely occupied by enclosed grass fields.

A well-adjusted primitive rural economy must maintain a proper balance between arable, pasture, and woodland, corresponding with three primary human needs—for vegetable and animal food and for wood. When the population grows so as to exceed a certain ratio to the available fertile land, these three uses of the countryside come into competition. If tillage is extended beyond a certain point pasture is unduly restricted, though this can be compensated for to a certain extent by bringing the feeding of sheep and cattle into the arable scheme—grazing on root

crops, clovers and stubbles, and stall feeding. If too much land is given to arable and pasture the area of woodland no longer supplies enough timber for construction and wood for fencing, for the making of implements and tools, and for fuel: recourse must then be had to importation. During the Middle Ages, as has been said, the proportions of land used for arable and pasture respectively fluctuated with the rise and fall of prices and the profitable export of cereals or of wool and cloth. At certain times the number of sheep kept was enormous in proportion to the human population. In the middle of the fourteenth century, with a human population of two million, the sheep population, maintained mainly for their fleeces rather than for mutton, is estimated at eight million in England alone, or four sheep per head of the human population.

But both arable and pasture were the enemies of forest, and there has been a steady depletion of woodland from the beginning of the disafforestation of the Norman Royal Forests right down to the present day. In the fourteenth century timber was already being imported in considerable quantity to certain parts of the country, especially the east coast, though there was still probably no *general* shortage in the fifteenth; but in the sixteenth century the dearth was certainly felt and in the seventeenth there was final exhaustion of the last native English forest reserves. In 1685 the use of foreign instead of English timber for the Royal Navy aroused indignation, but Pepys showed that the supply of English oak planks suitable for large ships was no longer adequate to the demand. It was the fuel required for iron-smelting and glass-making that led to the great depletion of high forest and native timber supplies in the sixteenth and seventeenth centuries, though these industries actually preserved woodland of a sort in the form of coppice into which high forest was converted, since in the absence of this demand the land would have been used for pasture or tillage.

A good deal of oak was coppiced in some parts of the country, the bark being used for tanning hides and the wood for fuel. But the main coppicing was of shrubs, particularly hazel, which had been very abundant in the underwood of the old oak forest, together with other shrubs

and such trees as ash and field maple which respond well to coppicing. Some of the oaks were as a rule left as standard trees, about twelve to an acre, a spacing which enables them to develop strong, widely spreading branches affording the curved timber useful in shipbuilding. In natural oak forest where the trees are closely set, and in plantations grown in "close canopy," the trees have long clean boles and narrow crowns, lateral branches being absent near the ground because the dense growth of young trees cuts off all but vertical light from the growing saplings. In the oak-hazel "coppice-with-standards," on the other hand, the wood is in "open canopy," each tree being well lighted all round and thus able to develop big lateral branches so that the crown is much wider and the trunk much shorter. At the same time the looser crown allows more light to penetrate and the growth of the shrub layer below is much more vigorous. This coppice-with-standards is still much the commonest type of oakwood in southern England and the midlands, and is well known for the glorious sheets of spring flowers, primroses, wood anemones, wood violets, and bluebells, that come into luxuriant blossom in the years after coppicing. In recent times the standard oaks—no longer profitable to grow—are usually neglected and in many existing coppices they are few or have disappeared altogether. These woods are now mainly used as pheasant preserves or fox coverts, but the coppice wood still has value for hurdles, fencing, stakes, faggots, pea sticks, and the like, though because of decline in the demand the coppice is now often not cut at the proper time, which is once every ten or twelve years, and becomes overgrown.

The increasing dearth of wood in the sixteenth and seventeenth centuries gradually led to the realisation that tree planting was necessary to replace depleted woodlands. All kinds of trees were actually planted in southern England in the seventeenth century, largely under the influence of John Evelyn and his friends, and much more for the interest of growing the trees than for the purpose of establishing timber-producing woodlands. Nevertheless Evelyn's influence notably helped to establish the *habit* of planting trees (though at first mainly as a hobby), and planting

on a larger scale reached considerable proportions in the eighteenth century, and continued through the nineteenth. The volume of planting, however, never attained proportions anything like adequate to the needs of the country, which imported more and more timber from abroad, largely soft woods (pine and spruce) from Russia, from the Baltic countries, and from Scandinavia, and later other kinds of conifer such as various kinds of pine, Douglas fir and Sitka spruce from North America, besides important tropical timbers like mahogany, teak, and rosewood.

In Scotland the history was rather different. The larger Highland valleys and glens still contained magnificent virgin forests at the beginning of the seventeenth century—of oak on the better soils, in sheltered situations, and at the lower altitudes, except in the extreme north, and of pine and birch on the poorer soils and at higher levels. These forests were "discovered" by exploiters about that time, and began to suffer ruthless destruction. Many were burned for charcoal, iron ore being brought to them for smelting. Much of the pine in Argyllshire was sold to Irish companies and iron ore brought to Scotland to use up the birch which remained. The great expansion of sheep farming which took place in the Highlands at the end of the eighteenth century and continued through the nineteenth led to the felling and burning of most of what remained of the Highland forests. The destruction thus lasted for nearly three centuries, and is being completed in our own day by the Forestry Commission, which is clearing what little remains of the native oak and pine in order to make dense plantations of exotic conifers.

In southern Scotland, on the other hand, the dearth of timber was felt a full century earlier than in southern England, and efforts to encourage tree planting are evident in records of the later fifteenth century. For a long time these efforts had little effect and the destruction of woodland continued, but towards the end of the sixteenth century certain Scottish landowners began to plant in earnest, and during the succeeding century their example was more widely followed, though it was not till the eighteenth that tree planting on a large scale became the fashion in Scotland, lords and lairds vying with one another in making

large plantations. In 1786 prizes were offered to farmers who should plant the largest numbers of oak, ash, and elm before a certain date. In the north Sir Alexander Grant began operations in 1716 and continued throughout his long life, reaching a total of fifty million trees. Scots pine (or Scotch fir as it used to be called in England) was the favourite tree with most Scottish planters. In 1705, for example, Lord and Lady Hamilton planted, for profit and with great success, 800 acres of pine on poor sandy soil. But both in Scotland and England several other kinds of tree were planted in quantity in the eighteenth century—birch, largely in Scotland, the other native hardwoods (oak, ash, elm, and a certain amount of beech), sycamore (not native but introduced long before), and the three continental conifers, larch, spruce, and silver fir. Of these last the European larch, first established at Dawyck in 1725, was much the most extensively planted, often as a substitute for the slower-growing oak. Larch does well in many situations where spruce makes indifferent growth and scarcely produces useful wood. Silver fir seldom makes really good trees in the British climates.

The great advance in planting during the eighteenth century was to a certain extent maintained in the nineteenth, but it went very little way towards rendering Great Britain independent of foreign supplies, even of timber which could quite well be grown here, because it was carried out almost entirely by private landowners. Returns from the planting of timber do not begin to come in for many years, and the yield in interest on the capital cost is low. In other words, "one plants for one's grandchildren and great-grandchildren." It is therefore properly the work of the State, or of very rich men. But until recently the State has never been willing to take its responsibility seriously and the rich men have generally preferred more lucrative investments showing quicker profits. The difficulty of importing essential timber during the war of 1914-18, however, roused the Government to the need of greatly increased native supplies, and in 1919 the Forestry Commission was established. This body purchased estates when they could be had cheaply, replanted existing woodlands, and planted on heathland,

moorland, or grassland. The trees it has used are mainly Scots and Corsican pine, Norway and Sitka spruce, Douglas fir, and Japanese and European larch. All but the Scots pine are exotic conifers, Douglas fir and Sitka spruce from western North America. The native hardwoods, like beech, oak, and ash, were comparatively seldom planted, because the great bulk of the modern demand is for the softwoods, which grow much more quickly than the hardwoods. The Forestry Commission plantations are not yet old enough to enter the softwood market on a large scale, and the value of the timber they will produce has not yet been adequately tested. At present the main market is in young pine for pit props, but in the future it is intended to produce large quantities of softwood for "rayon" and other industrial uses. The Commission people are thinking more and more in terms of the bulk of cellulose [1] produced by their "crops" rather than of wood as wood.

The Forestry Commission makes dense plantations of these conifers with varying degrees of success, sometimes on the sites of old deciduous woods, ringing the oaks to kill them, sometimes on grassland formerly used as sheep pasture, sometimes on heathland or partially drained wet moorland. The general result is to alter entirely the face of the landscape, destroying the old natural and semi-natural vegetation which has been gradually moulded through the centuries, and substituting artificial woods which do not harmonise with the native scene. It is widely felt that the Commission's activities have not paid sufficient attention to other interests, and that much more correlation of different possible uses of the land, not only economic, but ecological,[2] aesthetic, and sentimental, is required. More will be said on this subject in the concluding chapter.

We may summarise the historical changes in land use in a few paragraphs. As the area of woodland gradually decreased during the mediaeval and the beginning of the modern period, there was of course a corresponding in-

[1] Cellulose is the main material of which plant tissues are composed.

[2] Ecology is the study of plants and animals as they exist in their natural homes, of their "household affairs" and of the communities they form.

crease of land devoted to pasture and tillage. When corn prices were high more land was ploughed, and when the wool and cloth industries prospered more was "laid down to grass" by sowing grass seed, or simply allowed to "tumble down to grass." The period 1250-1350 is said to have been the most prosperous century of English mediaeval agriculture, in which the largest quantities of corn were exported. "Waste" common land in which the people (the local "commoners") had rights of grazing and wood collection was increasingly enclosed as time went on, culminating, as we have seen, in the Enclosure Acts of the late eighteenth and early nineteenth centuries which led to most of the remaining common land, including practically the whole of the "open fields" cultivated in common by the villagers for many centuries, being alienated and enclosed.

At the end of the seventeenth century an estimate of the proportions of land in England and Wales used for different purposes gives, in very rough figures, 28 per cent. to arable, 31 per cent. to grassland, 16 per cent. to woods, forests, parks, etc., and 25 per cent. to heath, moor, and mountain land. Comparing this estimate with the figures of 1939 (p. 1), it is seen that the grassland substantially increased, arable increased, though much less (until the period of the late war), and the last two categories greatly diminished, mainly through enclosure and conversion to arable or "permanent grass." There has thus been a notable reduction in the area covered with natural vegetation.

The trend towards grassland was already marked in early times—as soon as human occupation began to influence the country at all extensively—owing to the suitability of the British climate for the growth of grass and for grazing during most of the year; in the later Middle Ages and in Tudor times, especially as a result of the stimulus to sheep rearing on a large scale provided by the prosperity of the wool and cloth trades. There were expansions of agriculture proper, i.e. tillage, in the thirteenth century and again in the seventeenth, when corn was once more exported. This revival continued during the eighteenth century, when two million acres are believed to have been added to the arable area, to provide for the

rapidly increasing population and even for export, e.g. from East Anglia to Holland. But after the repeal of the Corn Laws in 1846 and the consequent wholesale importation of cheap wheat from America the trend towards grassland was resumed, and after the 'seventies the arable acreage steadily declined and the area of "permanent grass" correspondingly increased. This modern increase of grassland was very rapid during the last half-century, with only a temporary check during the war of 1914-18. But in the Second World War, owing to the acute demand for home-grown food, a great deal of "permanent grass" has been ploughed up and successfully converted to arable (see p. 2). Owing to the depression of the whole agricultural economy up to 1939 much of the "permanent" grass had been badly neglected, and was in very poor condition, lacking manure and seriously "undergrazed," leading to invasion by bushes and other "weeds" and to the production of coarse unpalatable herbage. Much low-lying grassland, too, was seriously in need of drainage. Very large capital expenditure is now essential if the English pastures, and indeed the whole of agriculture, are to be permanently restored to efficiency.

The story, then, is one of the gradual conversion of a country originally covered with forest all over the southern lowlands (except the fens and marshes) and on the valley sides of the north, with moorland or bog above the forest limits on the mountains, to a pastoral and agricultural country in which sheep rearing and to a less extent cattle raising were pursued side by side with corn growing. In the later phases tillage declined and grassland came to predominate more and more. Meanwhile the native woodlands very largely disappeared, though some remained, most of the southern oakwoods being maintained in the modified form of coppice-with-standards. Planting, at first of native trees, but in later times increasingly of foreign conifers, was always quite inadequate to meet the ever-increasing demand for wood, until the State undertook a few years ago to plant for national needs. The new plantations are almost entirely of exotic conifers and the woods they are producing are quite alien to our native landscape.

Changes in Population

In the picture I have tried to draw, the immense growth of towns and cities in the nineteenth century, and the twentieth-century suburbanisation of great tracts of country, not only on the outskirts of existing towns but on "building estates" in rural areas, have been deliberately omitted. The population of England and Wales increased from about 2 million—the vast majority rural—in the fourteenth century to perhaps 3½ million at the beginning and 6 million at the end of the seventeenth. Of the 9 million people at the end of the eighteenth century 78 per cent. still lived in the country. During the nineteenth century, as a result of the industrial revolution and the great increase of national wealth, the population more than trebled. This enormous increment was entirely urban, and very largely sustained by imports of food from abroad, so that the divorce from rural life became almost complete. The strictly rural population actually decreased during the century owing to the higher wages to be had in the towns, and later to the general decline of agriculture. The result was inevitably a disintegration and decay of rural economy. The change from an agricultural to an industrial and commercial, from a rural to an urban people, is of course the leading feature in social and economic English history during last century. But the actual spread of building, except in so far as it directly destroys the countryside, has only affected its character in minor ways.

To-day we have a population which has become almost static in numbers and is probably on the verge of a steep decline in the near future. The fate of England's green and pleasant land under such conditions we shall consider in our final chapter.

CHAPTER III

CLIMATE AND SOIL

DIFFERENT kinds of plants vary, of course, enormously in their preferences for different kinds of climate. Everyone knows that palms do not grow naturally in cold countries, nor cactuses in wet ones, nor oak trees in the tropics. All kinds of the higher plants grow wild only in climates they may be said to "like," i.e. where the temperatures at different times of the year and the amounts of moisture in the air are best suited to their life economy. But some of them can be made to grow outside—though not too far outside—the range of the climate they prefer. Thus the wild wheats from which our bread wheats are derived are natives of south-western Asia, but wheat is successfully cultivated, as we know, in the markedly different climate of western Europe. That is partly, no doubt, due to the creation through crossing and selective breeding of new strains which are better adapted to the new climate, but it is largely a matter of protecting the cultivated plant from the competition of the wild plants that are really at home in that climate—for example, keeping the wheat field reasonably free from weeds. If this is not done the wheat plants are eventually choked and die out. But you cannot grow wheat successfully in the wet tropics, nor cactuses in an English garden, however carefully you protect them—the climate is too violently different from that to which the plant is suited or adjusted.

The British Islands share in the general climate of north-western Europe: in other words, their climate resembles those of southern Norway, Denmark, Holland, Belgium, and northern France. Northwards along the length of Norway the lower average temperatures and the longer winters gradually lead to arctic conditions. Southwards, along the west coast of France, the higher summer temperatures lead towards the western Mediterranean climate. In spite of these differences of temperature due to latitude, the whole range of climate along the western coastlands of Europe is

what is called *oceanic*, and in this case *Atlantic*, because the dominant factor is the prevalence of south-westerly winds from the Atlantic Ocean, reducing both winter cold and summer heat and increasing the moisture of the air. On the coasts of the narrow seas—the English Channel, the Irish Sea, and the southern part of the North Sea—owing to the daily sea breeze, the climate has something of the same character, though to a much less marked degree than on the Atlantic coast, and may be called *maritime*.

Eastwards, as we pass to the interior of the European continent, where the moderating oceanic winds have less and less influence, the summers gradually become hotter, the winters colder, and the air on the average drier—the climate gradually changes to the *continental* type. Over the flat lands of north Germany and Poland, however, where there are no mountain barriers to interrupt them, the westerly winds carry the milder western climate, and with it the corresponding vegetation, far into the continent, though in constantly diminishing degree.

Lying as they do between the 50th and 60th parallels of latitude, and subject for most of the time to the warm Atlantic winds, the British Isles are characteristically *temperate*. How much the oceanic winds and to a less extent the ocean drift from the south-west, often miscalled the Gulf Stream, contribute to their temperateness is clear from the fact that Labrador, which lies across the Atlantic in the same latitude but outside the influence of the warm winds and the warm ocean current, has a subarctic climate. The general temperateness of our climate, expressed in the relative mildness of the winters and the relative coolness of the summers, is not infrequently interrupted by the intrusion of severe winter cold when the normal winter continental area of high barometric pressure (anticyclone), stopping the south-westerly winds, extends over our islands. Exceptional heat in summer is usually due to the formation of a more local and temporary anticyclone over or in the neighbourhood of this country. The other outstanding feature of the British climate is the general dampness of the air, also due to the Atlantic winds, which carry much water vapour from their long passage over the ocean.

Much of western Europe, some distance from the actual

coasts, has a modified oceanic climate, intermediate between the extreme oceanic and the continental. This may be called *suboceanic*, is not so wet, and has warmer summers and colder winters than the oceanic west coast climate. Away from the actual coast, eastern Ireland, the English midlands, and much of eastern and southern England, the lowlands of northern France, the Low Countries, and north-west Germany, have this type of climate; and eastwards through north Germany and Poland it gradually changes to the continental type.

All this applies primarily to lowland country. On hills of any considerable height the climate changes as one ascends. At the higher levels there is a general lowering of temperature, increase of rainfall and air humidity, and much stronger winds. In Great Britain the main hill masses are in the west and north, and the western high land cuts off some of the drift of moist warm air from the Atlantic, increasing the difference between the extremely oceanic western coastal climate and the suboceanic climate of the central and eastern lowlands.

Thus, though the whole of the British Isles may fairly be said to have an oceanic climate in the wide sense, we can distinguish *regional climates* (or subclimates) within their area: first, the *extremely oceanic climate* of western Scotland with its numerous islands, of western Ireland, of the Scilly Isles and Cornwall, and to a lesser degree the whole of south-west England and western Wales; secondly, the *suboceanic climate* of the midlands, eastern, and most of southern England; thirdly, the colder *northern climate* of northern England and most of Scotland, determined by the higher latitude and largely also by the great masses of high land—the Scottish Highlands and Southern Uplands, the Cheviot Hills, the Cumbrian Mountains, and the Pennines. To these three we may add the *arctic-alpine climate* of the upper parts of the higher mountains—above 2000 and especially above 3000 feet. This is marked by great increase of rainfall, cloud and fog, lower temperatures and much stronger winds, but more intense sunshine on clear days, and by a special flora and vegetation depending on these factors.

These regional climates are not, of course, separated by

sharply marked boundaries, but grade into one another by imperceptible transitions, except where a marked physiographical feature such as a steep and lofty hill range determines a sudden change of climate between the two sides. Also there are many areas of strictly *local* climate, determined by physiographic features such as protective hill ranges or nearness to the sea, as for example the notably mild climate of the shores of the deep bays in north-eastern Scotland—the Moray, Cromarty, and Dornoch Firths—within the northern climatic region. Local variations of climate extend indeed to much smaller areas than these. A valley open to the warmer and protected from the colder winds (especially the side facing south), an exposed wind-swept hill, a basin where cold air lies, all have local climates differing markedly from the general climate of the surrounding country. And smaller details still—down to the very smallest, such as the protection of an outstanding rock from sun or from wind—may bring about differences of climate within a few square yards—*microclimates* as they are called.

All these differences of climate affect the distribution of plants and vegetation. The great majority of the species of British flowering plants are common to the suboceanic regions of north-western Europe; and the leading types of natural and semi-natural vegetation are the same, with some modifications due to the position of Britain on the north-western oceanic limit of the continent. The flora and vegetation—based on deciduous (mainly oak) forest and the grassland derived from it—of the southern, eastern, and midland British lowlands are a detached and impoverished part (for not nearly all the continental species are present) of the flora and vegetation of the western European lowlands. In Scotland, especially on the hillsides, the original forest type is different—birch and pine forest corresponding with that of central Scandinavia. In the extreme west the blanket bogs [1] represent a third kind of vegetation, paralleled in the equally extreme oceanic climate of western Norway. Between the blanket-bog region and the other two lies a hill and mountain region in which the prevailing type of vegetation may be called broadly "*moorland*," and

[1] See p. 189.

the climate is intermediate between the extreme oceanic, the suboceanic, and the northern.

Of course the whole surface of the country in the different climatic regions is not covered by these "climatic" types of vegetation—apart altogether from the far-reaching changes brought about by human activity. Oakwood extends to the sheltered glens of the northern Highlands and to the well-drained sheltered valley sides of western Ireland, and differences of altitude, exposure, and slope bring moorland into the oakwood, birchwood, and blanket-bog regions. Extreme soil conditions also prevent the development of the characteristic climatic type of vegetation. Thus in the suboceanic climatic region marshes and fens occupy permanently waterlogged soil, and beechwood or ashwood rather than oakwood grows on shallow, highly calcareous soil.

Soil type is in fact the other great factor, second in importance only to climate, determining the distribution of natural vegetation and of the plant species of which vegetation is composed. Soil is the thin surface layer of the earth's crust in which plants are rooted, created by the modifying influences of rain, frost, sun, and vegetation on the mineral material of the crust. The kind of natural soil produced depends first upon the kind of subsoil or "rock," a term geologists apply not only to "rocks" in the ordinary sense, i.e. hard rocks, but to all the different constituents of the earth's crust even when they are soft like clays or incoherent like sands; and secondly upon climate. According to the rocks from which they are derived and their corresponding textures and chemical composition, soils may be roughly grouped into clay soils, silty soils, sandy soils, loams, and limestone soils, to which must be added peat soils derived not from a rock but from partly decayed vegetation compacted into a coherent mass.

Clay soils have a large proportion of very fine mineral particles consisting of complex hydrated aluminium silicates. These particles are extremely coherent in the solid state and hold water very tenaciously. When dried out a clay soil shrinks and cracks, setting hard like a brick. With excess of water it swells and becomes a slimy mud. Clay soils are poorly aerated and thus physically unfavour-

able to the root systems of many plants, since these require oxygen for respiration, and many species cannot easily grow in clay; but they are often rich in the mineral elements that plants need for food. Clay is a cold "late" soil since the large amount of water which it retains prevents it from warming up quickly in the spring. A *sandy* soil has the very opposite characters. It consists largely of relatively big particles, usually of silica (quartz), which do not stick together, so that the relatively large spaces between them contain a lot of air; and the soil has little power of retaining water. Sandy soils also are often poor in plant foods and are thus "hungry" soils—hungry both for water and manure. A *silty soil* has a preponderance of particles of size intermediate between those of clays and those of sands, and correspondingly the soil has intermediate characters, and is favourable to many plants. A *loam* is a soil containing a good mixture of particles of different sizes, so that it has more coherence and holds water better than sand, besides possessing more mineral plant food, but also contains more air then does clay between its larger particles. Thus loams are by far the most favourable soils for the growth of the great majority of plants.

The mineral plant foods referred to contain the metallic (basic) elements: calcium, magnesium, potassium, and iron, which, with nitrogen, sulphur, and phosphorus (coming directly or indirectly from organic substances), and carbon, hydrogen, and oxygen (obtained from the carbon dioxide of the air and from water), and minute quantities of other mineral elements, are all essential for building up the bodies and carrying on the lives of plants.[1]

Of these elements, calcium plays a predominant part in the soil itself. Its presence in adequate quantity and appropriate form neutralises the acids constantly liberated by decomposing plant bodies and it also causes the aggregation into lumps or "crumbs" of the excessively fine clay particles, thus "improving" the texture of a clay soil and

[1] Besides these "essential" elements of plant food it has recently been shown that extremely minute quantities of other elements—known as "trace elements"—such as boron and manganese and various others, are also necessary to many if not all plants.

rendering it much more favourable to plant life. All soils contain a certain amount of calcium, enough for the nutritive needs of the plants themselves, but much more than this minimum is required to produce beneficial effects on soil reaction and texture. A large proportion of British soils are "deficient in lime" in the agricultural sense and are improved by the addition of lime or powdered chalk. This is partly because many British rocks are themselves deficient in lime and partly because in the cool and rather wet climate of much of the country the rain, carrying carbon dioxide, dissolves and washes or "leaches" out the calcium salts from the upper layers of the soil.

Limestone soils form a class by themselves. Here the soil is impregnated with the calcium carbonate of which the parent limestone is mainly composed. Since calcium carbonate is soluble in rain water bearing carbon dioxide in solution, the soil is constantly saturated with an alkaline solution of lime. Insoluble mineral particles, of clay or sand or silt or a mixture, are present in a limestone soil in amount corresponding with the insoluble constituents of the parent limestone—abundant in an impure limestone, very little in a pure limestone like the chalk, so that the mineral framework of a limestone soil may be very scanty indeed above the rock. Limestone soils are thus thin, and dry because of their thinness and of the permeable rock below through which water readily escapes, but they are favourable to many plants in a sufficiently damp climate. Plants which habitually affect limestone soils are called *calcicoles*. Examples are traveller's joy (our native species of *Clematis*), wayfaring tree, spindle tree, rock-rose, several kinds of orchid, and many others. The strong alkalinity of these soils makes them uninhabitable for some other species, which are restricted to acid soils and are known as *calcifuge* plants. Of these our native heaths are good examples.

Peats contrast sharply with the other soil types because they are purely *organic*, being formed in fens and bogs (see footnotes, pp. 3 and 4) by the partial decay of many generations of plants and the accumulation of the resulting organic substance. Typical wet peats begin to form on soils saturated with water and thickly inhabited by plants. As the first plants living on such a soil die they decay

partially, but not completely, because of the lack of oxygen in the waterlogged soil; and their partly decayed and disintegrated dead bodies remain and form the substratum on which succeeding generations grow. This process is constantly repeated, so that an organic soil (peat), which may be many feet in thickness, is produced, the lower layers compressed beneath the weight of the upper. Such peats, formed under these waterlogged conditions, only continue to accumulate while they remain saturated with water for most of the year. If the surface dries out, the fen or bog plants inhabiting the wet peat cannot maintain themselves and are replaced by different species, while the substance of the peat begins to disintegrate.

Many peat-forming plants lose their structure more or less completely in this process of partial decay, but others, particularly bog mosses, may retain it indefinitely, and the species of bog moss may be recognisable in the peat after a great lapse of time. The hard woody or fibrous parts of other plants are also preserved, so that the plants to which they belonged can be identified, and we have already seen how pollen grains caught in the bog surface are preserved in peat for many thousands of years (p. 4). The preservative properties of bog peat are well known. "Bog oak," the carcasses of animals, wooden tools and implements, ornaments, and all sorts of other objects are found in bogs in a remarkably fresh condition. A perfectly preserved Roman soldier in full equipment was once dug out of a Yorkshire bog.

Fen peat and bog peat (see pp. 3 and 4, footnotes) are widely different in nature. Fen peat is formed in basins where the soil is waterlogged with alkaline (usually calcareous) ground water, draining from calcareous or other basic rocks (limestone, basalt, etc.), and this neutralises the acids formed during decay of the plants, and often leads to disappearance of their structure, so that fen peat is structureless and usually black. Bog peat is formed in the presence of water destitute of lime and poor in mineral salts, either water draining from rocks poor in these salts or rain water. It varies in texture and colour according to the plants of which it is mainly composed, and the more recent bog-moss peat is often quite light in colour, with the structure of

the bog mosses perfectly preserved. Bog peat is acid in reaction because there is nothing to neutralise the acids liberated by the dead plants.

A kind of peat may be formed under *dry* conditions. When there is not enough water present in the soil for the ordinary process of decay which leads to complete destruction of the debris of dead plants, the dry plant debris accumulates and forms a thick layer of "dry peat" or "raw humus," particularly when the debris is specially resistant to decay, as on the floors of heaths and of many coniferous woods, such as pine or spruce woods.

All but the rawest soils, freshly formed from the original rock or loose mineral deposit (such as blown sand or riverside alluvium newly laid down), contain a greater or lesser quantity of *humus*, the remains of plants which have lived on the soil and are in process of decay. The *rate* of this decay varies very much according to the conditions under which it occurs. At the one extreme, as we have just seen, it is arrested very soon, so that the partly decayed debris continuously piles up and forms peat: at the other, as on the floor of a tropical rain-forest where the temperature is high and steady all the year round and there is a good supply both of water and oxygen, the decay and destruction of humus is so rapid that in spite of the masses of dead leaves and twigs falling from the trees, very little is present at any time. In most English woods an intermediate condition is seen. After the autumn leaf-fall the dead leaves lie on the ground through the winter and even later, and are gradually converted into humus which is incorporated with the mineral soil below, largely through the action of earthworms, which drag the dead leaves down into the ground and are continually passing the humus through their bodies. The humus is also attacked by various fungi, and especially by certain bacteria which finally complete its disintegration. Ultimately the great bulk of the humus, consisting of the cellulose framework of plant tissues, is converted into carbon dioxide and water. But by the time this has happened a lot more leaves have fallen and are in process of conversion, so that a considerable amount of humus is always present in the surface soil. Humus of course contains compounds of nitrogen, sulphur,

and phosphorus, and such mineral elements as calcium, magnesium, potassium, and iron, all of which, as we have seen, are vitally important elements in living plants; and these compounds are broken down, mainly by the action of soil bacteria, into simple forms which plants can readily absorb and use.

Humus is an extremely important constituent of soil for more than one reason. In the first place, it is the most immediate source of the plant foods that have to be absorbed from the ground, since these foods are already in the plant tissues which are converted into humus and their elements can then be used again by the plants growing on the soil containing humus. Plants living on raw mineral soil containing little or no humus have to get their food direct from soluble constituents of the mineral soil, which is poor in some of them, such as nitrates; but when the soil is already rich in humus they can get it in the forms and more or less in the proportions they require, since these have already been selected by their predecessors, the plants from which the humus is derived.

Secondly, humus has important physical effects on the mineral soil. It "opens" the texture of clay soils and thus leads to better aeration. Like clay, it is retentive of water and thus increases the water-holding capacity of sandy soil. Together with the clay in a soil the humus forms a complex, known to students of soil as the "weathering complex," in which all the important chemical processes of the soil are carried out in watery solution.

Humus varies a great deal in nature, partly because of the different kinds of vegetation from which it is derived and partly owing to its interactions with the different mineral soils with which it is incorporated, and again to the different climates in which it is formed. "Mild humus" or *mull*, of which leaf mould is a good example, is formed where the conditions are most favourable to plant and animal life in the soil, where temperature is moderate (or high as in tropical forests), aeration good, moisture adequate but not excessive, and there is an adequate supply of nitrates and of the basic "ions" of calcium, magnesium, and potassium, as in an English deciduous wood on good loam soil. Here the autumnal leaf-fall supplies abundant

litter which is gradually converted into humus by the activity of the soil animals and plants—earthworms and other invertebrates including protozoa (unicellular animals), fungi, algae, and especially bacteria, some of which form the nitrates on which the higher plants depend. The bacteria are more abundant than fungi, which are kept down largely by the protozoa. All these soil organisms themselves find good conditions of life and abundant food in such a soil, and suitable plant food is constantly being liberated from the humus for the higher plants. It is for all these reasons that "leaf mould" (mild humus) is a good manure for garden soils.

"Raw humus" or *mor* is formed under less favourable life conditions—in cold climates and on soils poor in basic ions, especially in calcium. Here the soil system is quite different. Earthworms are absent, and other invertebrates and bacteria scarce, while fungi are more abundant. The process of humus turnover is much slower, so that the humus tends to accumulate and is more acid because of the deficiency of bases. Nitrates are scarce or absent and plant growth less varied and luxuriant. Mor soils bear a rather specialised vegetation of "calcifuges," since a great many species are more or less excluded. Mor soil occurs on heaths and moors and in many coniferous woods, and the tough resistant nature of conifer "needles" and of the leaves and twigs of heath plants contributes to the slowness of their decay. On the floor of a pine wood you find a thick layer of dead dry pine needles, passing down into a compact layer of peaty humus (mor) consisting of half-decomposed needles.

Finally, *water* is of course an all-important constituent of soil. Every chemical process which goes on in soil takes place "in solution," i.e. it requires water as a medium, and the higher plants absorb and evaporate very large quantities of water. If soil is too dry the life of all the organisms that inhabit it is checked; and if it is too wet and the water is stagnant, the resulting exclusion of air renders it unfavourable or impossible for many plants and animals.

The following paragraphs are rather technical, but some understanding of soil structure and its relation to climate

is of assistance in understanding the distribution of natural vegetation.

Soil is not an incoherent mass of mineral and organic particles: it has a definite *structure*. An important factor in shaping the structure of a soil is the *climate* in which it is formed, particularly the temperature, the amount and seasonal distribution of rainfall, and the ratio of precipitation (rainfall, dew, and snowfall) to evaporation (P/E), which partly depends on the prevailing temperatures of the air. All natural soils have a more or less *stratified* structure: in other words, a natural soil has a number of more or less well-defined layers, or *horizons* as they are technically called, from the surface down to a certain depth. These are formed by the action of sun, water, frost, etc., acting from the surface downwards. Besides these climatic factors, the vegetation growing in the soil influences stratification through its contribution of humus. The series of horizons is called the *soil profile*.

In dry hot climates, where evaporation tends to exceed precipitation, i.e. P/E is low, the net movement of water is usually upwards so that the surface layers of soil tend to "dry out." In wet cool climates where rainfall is copious and evaporation slight so that P/E is high, the movement of water in the soil is usually downwards. The downward percolation of water "leaches" the surface layers of soil, dissolving their soluble mineral constituents and carrying them down together with soluble humus material, and also the finer mineral particles of a mixed soil such as a loam, from the surface to lower levels. At the same time a layer of raw humus or mor tends to form and to remain on the surface, because the humus is not actively disintegrated in the cold wet conditions which are unfavourable to the life of soil organisms. This is especially marked where the soil is poor in nutritive salts. Below the impoverished uppermost layer of mineral soil (technically called the *A* horizon) the soluble humus material which has been carried down is deposited again and often forms a well-marked dark horizontal band (technically known as the *B* horizon). Sometimes this is quite hard and is then called *moorpan*. Below that again is often another (reddish) layer (*B* 2) in which iron salts are deposited, and then we

come to the unaltered subsoil or rock (*C*). This type of soil is called a *podsol*, from a Russian word meaning *ash*, because the impoverished surface layer of mineral soil (*A* horizon) is typically very friable and pale grey or whitish in colour. Podsols are characteristic of our cool and wet northern climates on all kinds of rocks except limestones. They are most easily formed where the rock is easily permeable to water, and especially where it is sandy. Many of the southern English sands form, or have in the past formed, podsols, though the climate is not a typical podsol climate, and in this southern climate quite a different soil is formed on the clays and loams. The conspicuously white sand of the *A* horizon can often be seen on the heaths of Surrey, Sussex, and Hampshire where the surface humus (mor) has been disturbed, and on the side of an old sand-pit the typical podsol profile may sometimes be observed. In the north, where most of the soils are podsols, these are formed on a great variety of rocks which vary in permeability but most of which are originally poor in soluble mineral salts. Many of the northern podsols are incomplete, but the tendency to podsolisation is everywhere evident. The natural vegetation of a podsol is commonly heath or moor, though the northern woods of pine and birch can maintain themselves on podsolised soils.

The characteristic type of soil formed on the loams and clays in the suboceanic but warmer and somewhat drier climate of the midlands and south is called *brown earth* or *brown forest soil.* Here the leaching is not so intense as in a podsol, though any lime that may have been present in the original "rock" has been leached out of the surface layer (*A* horizon) and carried down to lower levels (*B* horizon). The humus is of the mild type (mull) and is incorporated in the surface layers of mineral soil. There is no layer of raw humus or mor on the surface, and no sharply marked dark band below as in a podsol, but there is nevertheless a *B* horizon, a zone in which salts carried down in solution from the surface layers by percolating water and also the finer insoluble mineral particles are concentrated. The "brown earth" type of soil is most characteristically formed on clays, and especially the less pure clays which contain coarser particles and yield a heavy

loam soil; but it is also formed on impure sandstones which contain a lot of finer particles and also yield loams—sandy loams. The natural vegetation is deciduous forest—in this country mainly oak forest. Brown earths include most of the "good" soils used for agriculture, which are generally loams, and were the first to be cleared for tillage. The stratification is not so strikingly conspicuous as in the sandy podsols and requires closer scrutiny to distinguish the different horizons. Besides podsols and brown earths blanket-bog peat may almost be considered the climatic type of cool and very wet regions, but its formation depends also on poor drainage.

Thus we see that there are two main factors responsible for the formation of a natural soil: first the nature of the rock from which it is formed, and secondly the kind of climate in which it is produced. In a given climate there is always a *tendency* towards the production of the corresponding climatic soil type, but this cannot be fully effective on extreme types of parent material. Thus a nearly pure coarse sand cannot form a brown earth.

There are several other climatic soil types (or "world groups" of soils as they are called) in regions of very different climate from that of the British Isles, for example the fertile "black earths" (chernozems) of southern Russia and the "laterites" of the Tropics, and the tendency to form a uniform soil type throughout a particular climatic region may produce the same general type from a great variety of rocks. But the particular soil formed necessarily depends also, as we have seen, on the materials present in the original rock. It is only where this material is mixed, comprising coarser and finer particles and a variety of chemical substances, that the climatic influences can produce a typical example of a climatic world group. If the rock is relatively pure, chemically and physically, for example a pure siliceous sand or quartzite or a very pure limestone with practically no earthy admixture, or again a pure clay with few coarser particles, the climatic factors cannot produce a typically climatic soil because they have not the necessary material to work upon. And even when a particular soil clearly belongs to a given climatic type, for example a "brown earth," its particular character may

vary from a heavy clay loam to a coarse sandy loam according to the rock from which it has been formed. In the British climate both of these will naturally bear oakwood with a number of trees, shrubs, and herbaceous plants in common, but the floras of the two will not be identical because many species "prefer" sandy soils and others "prefer" clay soils.

The climatic factors cannot produce the corresponding soil type in its full development until they have been working on the raw materials of soil for a considerable time, the duration of which varies according to different conditions. When this development is complete the soil is said to be mature. A great number of recently deposited British soils are still *immature*, and some of the soils laid bare by the disappearance of the Pleistocene ice sheets ten thousand or more years ago are not even yet fully mature.

Besides the climatic "world groups" of mature soil found within the British Isles there are a number of other soil types which depend for their formation upon local conditions—special kinds of rock and situation, or the height and nature of the ground water. Of these the soil of steep limestone slopes such as the escarpments of the chalk in southern England is an outstanding example. The characteristics of this shallow limestone soil (*rendzina*) have already been referred to on p. 32. The surface soil is largely composed of a dark stable humus constantly saturated with calcium carbonate and with many free particles and small lumps of chalk. There is little or no leaching and no *B* horizon, the rain water quickly escaping down the slope and through the very permeable rock. The surface soil is often directly underlain by the disintegrated surface of the chalk; though there may be a thin layer of reddish-brown loam between the two. Such a soil is said to be "permanently immature" because the nature of the rock and the quick run-off of rainfall prevent its maturation by the climatic agencies.

Meadow soils are formed below a grass cover on river alluvium subject to flooding, so that the water level—never very far below the surface—constantly rises and falls, keeping the soil aerated, while the flood water brings fresh

silt bearing nutritive salts. The texture varies: very often it is intermediate between fine sand and clay (silty soil, p. 31). Meadow soil is very fertile and very rich in humus formed from the decay of the numerous fine roots of the grasses which inhabit it. If the soil is thoroughly drained leaching begins and a brown-earth profile will be developed. If it is continuously waterlogged, marsh develops; and if silting is stopped, *fen peat* (already described on p. 33) will be formed.

Raised-bog peat (see p. 184) is of the same general acid type as blanket-bog peat. It is formed on the top of fen peat if this grows up out of reach of calcareous ground water but remains waterlogged, and may reach a depth of many feet.

There are several other types of soil dependent on local topographic factors. The most important of these are the *maritime soils* and the *mountain soils*, neither of which can become mature because the constant operation of wind or salt water in the first case and of the severe mountain climate in the other, holds up the processes of maturation. Young sand dunes are perpetually changing in form through the deposition and removal of fresh loose sand by the wind. If they become permanently stabilised they behave like an inland sand. Salt-marsh soils are subject to the tides, and the action of these, with the salt they bring, gives salt marshes their characteristic soil and vegetation. In texture they vary from sand to clayey mud. Both freshly blown sand, and sand and mud periodically covered by the tide, bear highly specialised vegetation (Chapters XV, XVI). Mountain soils are continually exposed to violent erosion so that they cannot mature, and remain, broadly speaking, as bare rock or loose mineral debris in which the severe action of frost produces special characters.

There are few if any countries which contain within so small a space a greater variety of soils than England possesses; and this applies especially to the English lowlands. The north and west, with Wales, Scotland, and Ireland, show much greater areas of more uniform soil. The English lowlands, that is to say the east, most of the south, and the midlands, are made of rocks formed during the

later geological periods (Secondary, Tertiary, and Quaternary). They may be classed together as *neogenic*, and are on the whole much softer than the older rocks of the west and north (*palaeogenic*), since they have not been so much hardened by extreme pressure and metamorphism (i.e. the change produced by the proximity of the very hot, "volcanic" material which has formed the so-called "igneous" rocks). These neogenic (Secondary and Tertiary) strata outcrop, i.e. appear at the surface, in bands, which are sometimes quite narrow and whose general direction is north-east and south-west across England, and they include limestones, sands, clays, and marls, which repeatedly alternate with one another. Overlying the bands of Secondary and Tertiary rocks are numerous glacial and post-glacial (Quaternary) sands, gravels, silts, and boulder-clays (both calcareous and non-calcareous) which were formed during the Ice Age or later and have been partly worn away, exposing the older strata beneath.

The result of this varied origin of the surface material is constant change in the lithological basis of the soil as one passes across the country, and corresponding differences in the arable soil, often between the different fields of a farm or even between parts of a single field. The fragments of natural vegetation which are left and the semi-natural vegetation vary in a corresponding way.

What has been written refers only to *natural* soils, untouched by man. In fact, of course, the great majority of existing English soils and many Welsh, Scotch, and Irish soils have been radically altered by change of the vegetation, by ploughing and draining, by manuring, and in various other ways. When a waterlogged soil is thoroughly and effectively drained the surface layers partially dry out and the soil becomes fit for general cultivation. Crops can be raised on what was wet meadow, marshland, or fenland, and, after appropriate manuring, on bogland. Ploughing destroys the natural stratification of a mature soil down to the depth to which the plough reaches, and the lower layers also are altered by the surface cultivation and manuring, and by the growth of the crops in place of the natural vegetation. This is because the lower layers of

soil are now altered in composition and better aerated, and percolating rain water carries down different substances in solution. The whole soil is (or should be) enriched with fresh plant foods over and above what is immediately required by the crop, and thus the "fertility" of the land is "built up." In these ways a brown earth soil which may give quite a good crop immediately after ploughing can yet be substantially improved for plant growth by suitable manuring, as shown by the weight and quality of the crops. A ploughed-up podsol yields an extremely infertile soil, but adequate manuring with lime, potash, phosphate, and nitrogen manures, as well as dung, may in time convert it into very good arable land.

CHAPTER IV

SEMI-NATURAL VEGETATION

The Human and Animal Factors

We have just seen that the great bulk of English soils have been so much altered by man's activities as to destroy many of their natural characters. Nevertheless we can gain no thorough understanding of agricultural soils unless we can trace them from the natural soils out of which they have been made. It is the same with vegetation. Sown crops and plantations of exotic trees have, of course, no relation to the natural vegetation they have supplanted, except that the planted crops and trees must be able to grow successfully in the same climate and in soil of the same origin as those in which the original vegetation lived. But much of the existing plant covering that owes its present form to man's activity does not consist of planted crops and alien trees: while there is very little untouched natural vegetation there is a great deal *derived* from native vegetation that has been more or less changed by human agency. All this we call *semi-natural vegetation*, and it is our object to understand how it originated from the truly natural plant covering that once occupied the country.

First, there are the deciduous woods of oak, ash, beech, birch, and alder. Here and there fragments of these are not only natural but practically untouched. Such fragments, however, are few and far between, found only in spots too remote to be worth exploiting or where the tree-growth is so poor that the wood produced is not worth cutting. More extensive are woods from which trees are taken or brushwood cut from time to time, but which are not exploited regularly and systematically so as to modify their character significantly. Such woods, which are still common on the western and northern hillsides, may be taken as natural to all intents and purposes.

But the great majority of our deciduous woods are less natural than that, though they may consist entirely or

almost entirely of native trees. A few—notably certain beechwoods—are regularly exploited but managed on what is known as the selection system, in which mature trees are taken out and replaced by "natural regeneration," i.e. the colonisation of felling gaps by self-sown trees. These woods retain a large element of "naturalness," but they are markedly different from entirely natural woods. For example, very old trees and their dead and rotting remains are absent, and extensive removal of mature trees may substantially modify the undergrowth.

A great number of woods are clear felled when the timber is marketable, and then they have to be replanted, for if the site is left alone it becomes covered with weeds such as brambles, and would take a very long time to be recolonised naturally by the kind of tree which was there before. Indeed, owing to scarcity of the necessary seed parents in the neighbourhood such recolonisation might never take place.

If a clear-felled wood is at once replanted *with the same kind of tree*, the planted wood, when it has grown up, is a typical "semi-natural" wood of the kind to which a large proportion of our deciduous woods belong. The soil, though it changes to a certain extent—e.g. by more rapid disintegration of humus—while it is freely exposed to the weather, remains essentially a woodland soil and re-acquires its full character as soon as the young trees have grown up. Certain plants, alien to the natural woodland flora, get in during the period of exposure, but they will tend to disappear when the trees have formed a closed canopy. The alien weeds are generally plants which require full light—at least for flowering and seeding. Their seeds are blown in or are carried in on the boots and clothes of woodmen and others. They had no chance of establishing themselves in the mature wood and they often do not survive the re-establishment of woodland shade. Nevertheless some may remain; but the bulk of the flora will again become a genuine woodland flora. The trees themselves will be even-aged since they were all planted at the same time, and hence the floor of the wood, if the soil is even and uniform, will tend to bear a uniform vegetation, and the diversity usually seen in a really natural wood will

be lacking. Very likely certain relatively rare woodland species occasionally found in less exploited woods will be absent because they have been destroyed during fellings or have died out while the ground was bare of trees, and have never returned.

A very common example of this type of wood is the oak-hazel "coppice-with-standards" whose nature and origin were described in Chapter II. These woods have often been uniformly planted with oak and hazel, sometimes on the site of an old wood, sometimes on grass or arable land; and when they are regularly coppiced they frequently possess a uniform woodland flora not very rich in species and marked by the dominance of one or more kinds of gregarious spring-flowering plants such as primrose, wood anemone, or bluebell.

When a felled wood is replanted with a kind of tree which is not the natural dominant in the particular region or on the particular soil the wood begins to lose the claim to be considered a semi-natural wood, though its flora will still be a woodland flora. The herbaceous vegetation of a wood is largely determined by the soil and may have comparatively slight relation to the particular deciduous trees which form the canopy, so that it may remain much the same after replanting, provided the planted trees cast shade comparable with that of the original natural dominants. But if the planted tree differs widely from the natural dominant, particularly if it is an evergreen conifer, the ground vegetation is completely altered and the wood becomes nothing but an artificial plantation. Such a conifer plantation (say of pine) cuts off light from the ground throughout the year and at once begins to alter the soil by the resistant nature of the litter. The result is usually to destroy most of the natural undergrowth, so that very few of the original species remain and the floor often becomes practically bare, covered with the deep litter of tough pine needles passing into raw humus below. Larch, being a deciduous conifer with comparatively soft needles, and not casting any deep shade, has a less profound effect on the undergrowth, especially if the soil is light, so that a sandy oak or birch wood felled and replanted with larch may retain its vegetation of bracken and bluebells.

Semi-natural Grassland

Far more extensive than the comparatively meagre deciduous woodlands that still remain are the semi-natural grasslands. Broadly speaking, these fall into two groups. First, there are the "rough grazings," most of which occupy hillsides—the chalk downs and the limestone and siliceous pastures of the northern and western hills—and also grass-covered and grazed lowland commons. Much of this land was formerly covered with forest, which was cleared to make room for sheep-grazing, and the grasses and other herbaceous plants which have come in place of the trees, and which are all native species, are only maintained by the constant pasturing. If these hillsides and commons are left ungrazed or are insufficiently grazed they are invaded by shrubs and trees when the necessary seed parents are present in the neighbourhood, by heather on sandy soils, or by "weeds"—coarse unpalatable grasses and other herbaceous plants. The rough grazings are no more than semi-natural in the sense that they would not be there if it were not for man and his flocks, but under these conditions, i.e. continuous grazing, their vegetation is entirely spontaneous.

Secondly, there is the so-called "permanent grass" which is enclosed and frequently manured. Permanent grassland forms part of our agricultural land in the broad sense and is by far the most extensive of any kind of vegetation in England and Wales (see p. 1). Most of it is used for pasture, but some for hay-making as well, and these uses may alternate in different years or in the same year when the aftermath of the hay crop is grazed. Very much of this grassland was formerly arable and has been "laid down" to grass (i.e. sown with grass seed) when arable crops became unprofitable. In war-time, when importation of produce is difficult, there is always a great ploughing up of grassland in order to increase the arable acreage. During the late war this effort was particularly vigorous and the area of permanent grass in England and Wales decreased from 64 to 40 per cent. of the farm area.

The grasses and herbs which occupy "permanent" grassland are all or almost all native, and they vary a great deal according to the nature of the soil and the amount of soil water, according to manuring, and according to grazing

regime. Since this grassland has usually been deliberately sown with grass seed it is clearly less "natural" than the rough grazings, but it is nevertheless fairly regarded as "semi-natural," for though it may have started with a particular seed mixture it always alters in composition as time goes on, some kinds dying out and other native species entering according to the play of the factors mentioned. It has been shown by exact experiment that a change in manuring alone or a change in grazing alone (sheep or cattle, grazing at different times of year) will completely alter the flora of a grass field.

The oceanic climate of the British Isles, its prevalent coolness, mildness, and dampness, is peculiarly suited to the growth of pasture grasses, which like frequent rain and can go on growing through a mild winter. Some of them come spontaneously, together with other plants, wherever ground is bared. Pasturing (or mowing) encourages them at the expense of many of the herbs, because most of the grasses increase vegetatively from the base of the plant by the growing out of buds ("tillers") which escape destruction when the herbage is cropped by grazing animals or cut with a scythe or machine. It is in this way that the continuous turf of a grass field or a lawn is produced, for the constant cropping or cutting, if not too severe, actually encourages the vegetative growth of the grasses by preventing their flowering, and the treading or rolling consolidates the turf.

So ubiquitous is grass vegetation as to make it almost true that if any piece of vacant land in the lowlands is left to itself and the spontaneous vegetation which appears is then pastured it will become grassland. Thus if an arable field is left unploughed and stock is turned in it "tumbles down to grass," though a pasture thus formed has not, of course, the initial advantage of being sown with the specially chosen grasses of a good seed mixture.

Thus it is grazing animals, aided by the British climate, that may be said to have created and to maintain the British grasslands, not only the rough grazings but the grass fields. Sheep and cattle, man's flocks and herds, have been the main agents, with horses, donkeys, and goats in very minor degree. Apart from these there are a few wild

herbivorous animals that have influenced our semi-natural vegetation to a marked extent, and of these by far the most important is the rabbit.

The rabbit is not an original native of this country, though it has been wild here for about eight centuries. It was introduced by the Normans both to England and Ireland from southern Europe. At first the wild rabbits were apparently scarce and fetched comparatively high prices, but by the middle of the fifteenth century they must have been very abundant judging from the enormous numbers used at feasts. In the following century the German naturalist Gesner described the immense abundance of rabbits ("copia ingens cuniculorum") in England. In the seventeenth century rabbits were highly valued as a source of both food and fur, and so they remained until quite recent years. In Scotland they were little known till the nineteenth century, when they must have increased very considerably, for they are now found throughout the country and on almost every island and islet off the west coast, though always introduced by man so far as records show. In England they have become a real and serious pest to agriculture and forestry by their attacks on growing crops and seedling trees, and they have destroyed the value of great areas of rough grazing, especially on the chalk downs, by eating down the turf so close to the soil that no larger animal can get any food. On the sandy soil of Breckland in south-west Norfolk and north-west Suffolk they have destroyed great areas of heath, converting it into bent-fescue grassland [1]—quite useless because it is eaten down to within half an inch of the soil surface—and the new pine plantations of the Forestry Commission have to be protected by rabbit-proof fences.

Constant appeals for systematic destruction of rabbits have been launched, but although spasmodic efforts were periodically made and local reduction or extermination effected, the animals always increased again and no permanent abatement of the nuisance was achieved. During the late war, however, the Ministry of Agriculture undertook a general scheme of rabbit destruction by gas-poisoning with much more success, but considerable numbers still

[1] See p. 169.

survive. Mr. J. Simpson, who knew more than most people about rabbits and their ways, pointed out, many years ago, that a really effective method of dealing with the problem would be to confine rabbits strictly to securely fenced warrens (which can be very profitable if properly constructed and managed) and to enforce under penalties the destruction of all rabbits found outside. The responsibility for this could be placed on landlords and their tenants, with any necessary help from a central authority.

One important point, commonly ignored by those who demand complete extermination but are not in constant touch with country-folk, is the part which rabbits play not only in providing sport easily accessible to almost all, but also food for larders which are none too well stocked. In spite of damage to crops there are farmers who would be loth to see rabbit-shooting made impossible, and there are poor countrymen of very various callings to whom the removal of all chance of snaring, trapping, or shooting a rabbit for supper or Sunday dinner would be a real deprivation. This may not be a valid argument against general effective extermination of rabbits, for the aggregate damage they do is undoubtedly enormous, but it is at least an explanation of the widespread want of enthusiasm for such schemes.

Rabbits can and do burrow in almost any soil, even tough clay or a surface coal seam, but they much prefer a naturally dry soil or a soft rock. Sand dunes, sandy heaths, and chalk downs are among their favourite habitats, and here they live in vast numbers. Nevertheless their incidence is unequal. Along the South Downs, for instance, there is little sign of them in some places, while in others they completely dominate the vegetation. This is probably mainly due to their local treatment by the landowners or tenants. In some places they are systematically trapped, in others preserved and even fed in the winter for the sake of the shooting. They never go farther for their food than they need, so that the ground surrounding an isolated groups of burrows on a chalk down shows a concentric zonation. Immediately around the burrows there is a ring of bare chalk stones thrown out by their vigorous hind feet, then a wide zone of turf eaten down to half an inch or

less, grading to herbage less severely nibbled, while at a distance of 100 yards or so there may be little evidence of rabbit-grazing. Where the groups of burrows are numerous the grazing ranges overlap, and in such a region many hundreds of acres may be rendered useless for sheep or cattle. Within the devastated area no seedling of a woody plant can survive, and any scrub that may have been present before the rabbit infestation became overwhelming has its lower branches eaten bare up to the height a rabbit can reach. Such an area has a most desolate appearance at all times of the year. On steep chalk slopes the scratching of the rabbits around their burrows, completely destroying the herbage, exposes the soil to erosion and rain-wash down the slope, and considerable areas may thus be denuded of vegetation and covered with fragments of chalk so that they show up from a distance brilliantly white on the hillside.

A number of plants are unpalatable to rabbits, some are only eaten if nothing better can be had, and others are never touched. Conspicuous among these last is elder, which seems never to be eaten: clumps of elder bushes often grow in the midst of burrows. Other rabbit-resistant woody plants are bramble and broom. Among herbaceous plants there are ground ivy, wood sage, ragwort, field and early forget-me-nots, wild mignonette, rock-rose, stonecrop, mullein, nightshade, hemlock, thistles, and stinging nettles. Several though not all of these are protected by coarse hairs, others are prickly or poisonous. The stems of deadly nightshade are sometimes gnawed through, rabbits being immune to the poisonous alkaloids they contain. On sandy heaths the young shoots of the common heather or ling are freely eaten, but not the waxy or the purple bell-heather. Bracken is always avoided, and this is a great advantage to the plant and helps it to spread over heathland and other light soils where many of the other plants are eaten. Sand sedge is eaten, but not by preference, only if nothing more palatable is to be had.

Both on sandy heaths and chalk downs the tall rabbit-resistant plants stand up conspicuously from the closely nibbled turf of rabbit-ridden areas—ragwort (which has increased enormously of late years and is so poisonous to

stock that it has become a serious pest), and in places nettles, thistles, mullein, black nightshade, etc. Such areas are both agriculturally useless and aesthetically depressing, and there is no doubt that they ought to be taken in hand. Some might be properly fenced and turned into useful and profitable rabbit-warrens. On others the rabbits should be exterminated and the land used for grazing, or, where the soil is deep enough, ploughed and cultivated, or planted with trees.

The crisp springy turf which covers much of the downs, and is so delightful to walk upon, owes its character to rabbit-nibbling, not where they are in the enormous numbers that cause the devastation described, but where they are still fairly numerous. Under sheep-grazing alone, and in the complete absence of rabbits, down pasture supports a deeper herbage and the turf loses its resilience.

Rabbits do considerable damage to woodlands by eating off the tops of tree seedlings and barking young saplings, especially in the winter when they are pressed for food. In these ways they play a part in hindering the regeneration of woods, though not nearly to the same extent as the voles and mice. They also affect our coastal vegetation where they inhabit the sand dunes in vast numbers, attacking not only the dune vegetation itself but also that of the salt marshes, certain species of which they nibble severely while of others they bite off the shoots and leave them lying. But so far as is known they do not appear to cause any major changes either in sand-dune or salt-marsh vegetation. Much of the damage that rabbits inflict on shrubs and young trees arises not from what they eat but from the need to wear down their continuously growing teeth, which would otherwise become so long that they could not feed at all.

Next to rabbits, and in woodland more than rabbits, mice and voles are the most important rodents in altering our vegetation. Of these the widespread and abundant species are the common vole, the bank vole, and the long-tailed field mouse. The last-named lives in woods, is nocturnal in its habits, and is probably responsible for the destruction of acorns and beech mast. The bank vole is omnivorous but probably mainly eats seeds, bulbs, and tubers. Though

primarily a grass-eater, it is very likely the common vole that is chiefly responsible for the destruction of tree seedlings. The doubt as to exactly which of these animals is responsible for different kinds of damage is due to the difficulty of directly observing their feeding habits, since they feed mainly at night. It is known, however, that as they tunnel through a woodland soil just below the surface humus they eat through the main root of any tree seedling they encounter, and that they also bite off the tops of tree seedlings above ground. And it has been shown more than once that mice or voles are responsible for removing or destroying acorns, great numbers of which lie on the surface in autumn. The whole lot may disappear within a short time, even those that are buried in the humus.

Mice and voles are certainly the main agents in preventing the natural regeneration of our deciduous woodlands. The only practical way to combat them would seem to be to encourage some of the various carnivorous animals and birds of which rodents are the natural prey, but on which ceaseless war is now waged by gamekeepers for the protection of their pheasants.

The wild populations of voles show cyclic variations in their numbers, and in the years represented by the peaks of the population curve these animals not only destroy tree seeds and seedlings but undoubtedly also a great deal of grass, as well as killing tussocks of rushes. The common vole has also been shown to alter vegetation dominated by the purple moor-grass (*Molinia*) in two separate localities in Wales and Scotland. When voles are excluded by narrow-meshed wire netting from a small area the *Molinia* within the netting grows more luxuriantly, accumulating more litter and forming a closer stand, the accompanying plants diminish in number, and the mosses, ordinarily forming a numerous and important element of the vegetation, practically disappear. This effect is attributed to the exclusion of the normal activity of the voles in making innumerable tunnels just below the surface of the litter, gnawing through the roots and rootstocks of the dominant grass and thus diminishing its vigour and making room for a more varied vegetation between the *Molinia* tussocks.

Hares, both the common and the mountain hare, are

quite destructive animals, but since they are not gregarious and do not occur in such enormous numbers as the rabbits they have no ascertainable general effect on vegetation. The same may be said of squirrels, both the native red squirrel and the naturalised American grey squirrel which has increased so greatly in recent years. They not only eat and store pine seeds, acorns, and hazel-nuts, but destroy the buds and young shoots, and bark the upper branches of the trees, though they have not yet been recorded as causing *widespread* effects on vegetation.

The Highland red deer, which are much the largest native British animals, on the other hand, do have a general destructive effect on tree vegetation. This is because they are naturally forest animals, but are maintained in very large numbers (there were said to be 150,000 head in 1928) in the so-called Highland "deer forests," which are really upland moors possessing little or no woodland. In summer the deer feed on the growing shoots of heather and on grasses, but in winter they descend to the valleys for shelter and feed upon twigs, bark, and any acorns and beech-nuts they can find in the woods, besides attacking gardens and field crops. The fragments of native birchwood still existing on the Highland hillsides suffer severely from their ravages; as the old trees die they are not replaced by saplings, which are destroyed by the deer before they reach maturity. New plantations in the Highlands always have to be fenced against deer.

Four centuries ago, when the Highland valleys and glens were filled with forest and the hillsides lined with pine and birchwoods, the deer, which naturally ranged between forest and moor, could find ample food in summer and winter alike. After the woodlands were destroyed, from the seventeenth century onwards, their food was seriously diminished; and especially in modern times, when the deer are preserved for stalking, the moors are seriously overstocked and the herds have become the enemies of all tree-growth in spite of a good deal of artificial feeding in winter.

The roe deer—much smaller animals—are found throughout the northern Highlands, but in much lesser numbers, since they are not preserved, and though they do a good

deal of damage to young conifer plantations both by rubbing against the young trees and rooting up seedlings and saplings with their antlers they have little general effect on the vegetation.

The existing fallow deer are not now native to Britain though their remains occur in inter-glacial deposits. They were probably re-introduced by the Normans and are now frequently kept in parks, whence they often escape and maintain themselves in well-wooded parts of the country. These semi-wild herds are very prolific and often become a serious nuisance to farmers and foresters, for they are as destructive to crops and plantations as the wild species, and big deer "shoots" are organised now and then. Several other kinds of deer are also kept in parks and likewise escape and do similar damage.

Certain species of birds have a considerable local effect on vegetation. Some that are locally very numerous may seriously diminish seed supply. Wood-pigeons and rooks, for instance, may add to the heavy destruction of acorns caused by the small rodents. The immense congregations of starlings roosting in winter in certain woods break down tree branches with their combined weight and greatly modify the undergrowth through the massive accumulation of their dung on the floor of the wood. The effect of bird excrement in completely changing vegetation is strikingly seen below the so-called "bird cliffs" on the sea-coast and outlying islands where enormous numbers of seabirds breed. The soil of such places comes to contain great quantities of organic nitrogen and only certain plants can grow there. The number of species, which include scurvy grass, campion, stinging nettle, annual meadow-grass, and some others, is very limited, but their growth is particularly luxuriant.

Of course an enormous variety of animals of all kinds, from mammals to insects and worms, affect the lives of plants in the most diverse ways, some harmful, some beneficial, by eating various parts of them, by pollinating the flowers, or by distributing seeds, but it is not with such actions, important as they are, that we are concerned here. The broad and direct effects of animals in *changing* the character of great areas of vegetation is confined to gregarious herbivorous animals when they are introduced in

great numbers to a country or region where they do not naturally belong. The great herds of bison that once existed on the North American prairies, the various kinds of buck and antelope of the South African veld, are found in relatively dry continental climates not well suited to forest growth but specially favourable to great grass-covered plains where these grass-eaters are perfectly at home. They do, no doubt, push back the forests on the edges of such regions and these tend to advance when the herbivores are diminished, but the animals fit the natural vegetation of their native regions.

The vegetation of England, which belongs to a natural forest region, has been changed through the centuries, first by man directly destroying the trees for the sake of their wood, and secondly through the agency of his flocks and herds for which he requires pasture. His introduction of rabbits had a similar though more local effect, and his unintentional favouring of the small rodents through the destruction of their natural enemies seriously interferes with the regeneration of woodland, while his preservation of red deer tends to convert Highland woods into moorland.

CHAPTER V

THE MOSAIC OF VEGETATION

Plant Communities and their Succession

In the preceding chapters we have considered the main causes of the existing diversity of vegetation, of the patchwork or mosaic which covers the surface of the land. Before the development of human control the vegetation pattern was much more uniform over wide stretches of country, its determinants being solely differences of regional or local climate, of soil type and soil water, and of physiographic features. Man began to break up this comparative uniformity as soon as he began to clear forest, to pasture his flocks and herds, and to sow his crops; and he has done this at an ever-increasing pace, so that in the countries of old civilisation and comparatively dense population most of the landscape bears little resemblance to its original state. Nevertheless behind all the radical changes which human activity has brought about it is usually possible to reconstruct approximately the original nature of the vegetation by careful study and comparison of the existing remains of natural vegetation, of the behaviour of the dominant plants, and of historical and prehistorical records.

In this chapter we shall consider the nature and status of the units which make up the mosaic of vegetation, whether natural or semi-natural, how far they are stable and how they may change from one into another.

Plants are essentially gregarious beings, growing together in masses which cover the surface of the land so as to form a continuous carpet in all but the most unfavourable climates and situations. Moreover, some species are so vigorous and successful that they oust direct competitors and *dominate* the vegetation over wide areas in which they find the conditions of life favourable. That is why we can speak of oakwoods, beechwoods, birchwoods, and pinewoods, of heather moors and of sphagnum bogs. In any piece of natural vegetation dominated by a single kind of plant there are practically always other kinds—often a

great number—associated with the dominant, growing under its shade, or in spaces left between the dominant individuals. These associated plants, though not dominant, find their life requirements satisfied in such situations, and the whole collection of them, together with the dominants, thus forms a *plant community*, in many respects comparable with a human or animal community. In an oakwood, for example, shrubs grow beneath the shade of the trees, woodland herbs below the shrubs, and mosses close to the ground. The particular species of shrub, herb, and moss vary to some extent according to the soil and other factors, but many of them are common to most oakwoods; and thus we can recognise an organised whole, the oakwood community, composed of the dominant oaks (without whose shade and the humus derived from their fallen leaves many of the subordinate plants could not grow or flourish) and the whole set of associated subordinate species. The same is true of other kinds of woodland, and, *mutatis mutandis*, of heaths, moors, fens, bogs, and so on.

The dominant plants of a natural community are in general the largest and tallest plants which can establish themselves and flourish in the particular habitat, because they overshadow the rest of the vegetation, excluding some species by cutting off the light, and favouring the growth of others which require shade. In a complex community like a forest, where there are distinct *layers* or *strata* of vegetation one below the other, we can properly speak of the dominants of each layer, for instance hazel in the shrub layer of an oakwood, wood anemones, primroses, or bluebells, or some other gregarious woodland plant in the herb or "field" layer, and different species of moss in the ground layer. The dominants of each layer control, to a certain extent, the vegetation of the layers below. Thus when the tree canopy is very dense the shrub layer is poor or absent, a close shrub layer will considerably diminish the luxuriance of the herbs, and when these last grow very thick there is little room for mosses. The plants of each layer have in general common characters of stature, constitution, and mode of growth, what is called a common *life form*. Deciduous trees, herbs, and mosses are outstanding examples of different life forms. Among herbs there are

many varieties of life form according to their particular construction and mode of growth.

Some plant communities are dominated, not by a single species, but by two or more species of the same or similar life form. In grassland, for example, there may be several co-dominant meadow-grasses, and in some woods there are two or more co-dominant trees. Within a major plant community there is often local dominance of certain species, other than the general dominant, within any one of the layers. This sometimes depends on minor differences of habitat and sometimes results from other causes. Very often such a local *plant society*, as it is called, contains associated plants not found or not so abundantly found in the general vegetation of the larger community within which the society exists. Other species may be rare or absent in the society but frequent in the general community. This is because the local dominant brings about special conditions within its area of dominance, or because the habitat conditions which suit it also suit the particular associated plants. Thus we have communities of different grades or sizes, the smaller often contained within the larger. In the same way our different types of deciduous wood—oakwood, beechwood, ashwood, etc.—form distinct communities (*plant associations*) within the larger community, often called a *plant formation*, of the deciduous forest of western and central Europe which is everywhere dominated by a very distinct type of life form, the deciduous forest tree.

Of course plant communities are not always perfectly definite entities with sharply defined boundaries. All kinds of plants grow in any place which they can reach and in which the conditions of life are sufficiently favourable to enable them to survive. Accordingly many plants that are not exacting in their requirements range through many different communities, and you often get a hotch-potch of such species, especially when a site has been recently cleared or disturbed. In such cases there may be no dominants and it is often difficult or impossible to characterise or name such a collection of plants as a definite community. And a perfectly well-defined community may show gradual transitions to other adjacent ones, either because intermediate habitat conditions exist towards the

boundaries or because one community is in process of invading and ousting an adjacent one. Again, many types of community show every grade of variation in actual composition, so that it may be hard to decide whether one should recognise one community with many varieties, or distinct communities. But the tendency to form distinct communities, which often possess considerable stability, as the result of the gregariousness of plants, of their varying life requirements, and of effective differences of habitat, is a perfectly definite and characteristic feature of vegetation; though plant communities are, on the whole, more loosely integrated units than, for instance, human communities.

The major plant communities which cover the earth's surface are stable forms of vegetation because they are closely fitted to the climates in which they prevail. If the climate of a region changes, the vegetation changes with it. Examples are found in the various changes of climate and corresponding vegetation that have occurred in Europe since the last Ice Age, as we learned in Chapter I. But there is much natural vegetation which is not stable, even in the same climate and on the same soil.

When a piece of bare ground is exposed, plants at once begin to settle on it, except in the most arid climates. The kinds of plants that come first and the rapidity with which they establish themselves and spread vary with the climate and the nature of the substratum. The first colonisation is often by lower plants—algae, lichens, and mosses—whose spores and other microscopic reproductive bodies are brought by wind or by water. This is seen especially on bare rock surfaces which are wet or damp for at least part of the year. On loose soil, such as bare sand, alluvial silt, or tidal mud, annual flowering plants whose seeds are also wind-borne or water-borne usually figure prominently among the pioneer colonists. The decay of the bodies of the first plants to settle contributes humus to the raw mineral soil and begins to improve it. The rain of air-borne, or the deposit of water-borne, spores and seeds continues, while the plants that are already established begin to reproduce themselves. Perennial plants take root and some of them spread vegetatively. In these ways, sooner or later, a closed carpet of vegetation is established.

Among the perennials the seedlings of woody plants—shrubs and trees—are found, and where these can take root and flourish they will, of course, eventually overshadow the lower-growing plants and kill out those which require full illumination. A number of phases of vegetation are thus successively established, usually in the order—lower plants, herbs, shrubs, and trees; and there is often more than one population of each of these life forms, for example birch before oak, and on chalky soils ash before beech. In all favourable climates woodland is ultimately established, and this will eventually be dominated by the tallest trees, casting the deepest shade, which can succeed on the particular soil and in the particular climate.

During the whole process, which may be complete in a few years or occupy many decades or even centuries, the soil is developing along with the vegetation. An original bare rock surface is gradually disintegrated by weathering and the action of the plant roots, and the mineral soil, whether formed *in situ* from rock or carried from elsewhere by wind or water, is constantly enriched with humus, which helps it to hold water. At the same time the soil gradually becomes stratified (see p. 37).

When the bare ground was originally submerged, as on the floor of a pond or lake, the early stages of colonisation are by water plants. When the ground level is raised to near the surface of the water, either by accumulation of plant debris or by silting, or by both together, reeds or bulrushes or tall sedges or water grasses, whose erect shoots grow high above the water, establish themselves and form a reedswamp. With further rise of the soil marsh or fen plants settle among those of the reedswamp and gradually supersede them. Above the water level shrubs and trees, such as sallows and alders, which can grow in saturated or nearly saturated soil, make their appearance, forming marsh or fen scrub or woodland. With further accumulation of humus or silting from flood water the surface layers of soil, now well above the winter water level, become drier and suitable for the invasion of other trees such as birch, ash, and oak; so that eventually a forest may be established which is dominated by the same trees as those which ultimately dominate the vegetation developed on dry land

from the beginning. In the series beginning in water humus is accumulated as on land, but here the soil becomes progressively *drier* up to a certain point, whereas in the dry land series it becomes *damper* owing to the water-holding power of the accumulated humus. Thus the two types of succession converge, and the *climax* community, as the vegetation ultimately developed is called, may be practically the same in both cases, though the early stages of the series were very different.

The processes briefly outlined in the last three paragraphs are called *succession*. It is not within the scope of this book to describe its varieties and laws in detail, but the nature and distribution of natural and semi-natural vegetation cannot be comprehended without recognition of the phenomena of succession and some understanding of the ways in which they are modified by human action.

Any particular successional series of plant communities, culminating in a climax, is technically called a *sere*, and the seres beginning on dry rock or soil are known as *xeroseres*, while those beginning in water are called *hydroseres*. All such complete seres leading from bare ground to the climax communities dominated by the largest plants are called "primary seres" or *priseres*. Complete priseres can rarely be traced in a country like England because man always interferes with them sooner or later, but fragments of priseres can often be detected and followed in various places. Much commoner are partial seres or *subseres* which begin from some intermediate stage brought into existence by human activity, such as a clear-felled forest which is recolonised by trees or an abandoned pasture invaded by woody plants. These subseres are never exactly the same as the corresponding part of a prisere, because the habitat colonised by the plants is, so to speak, artificial, and the conditions are thus different from those produced in the course of a natural sere.

Furthermore, any continued incidence of human activity on the vegetation *deflects* the sere from the course which it would otherwise pursue. Thus if an East Anglian fen vegetation dominated by sedges is cut, the normal succession to fen scrub and woodland is interrupted by the destruction of the woody seedlings. If the cutting is

repeated often enough—say every two years—not only are woody plants prevented from entering the succession, but the sedges (*Cladium*) are so severely handicapped by the destruction of their evergreen shoots that they gradually give way to the purple moor-grass (*Molinia*), which can tolerate the repeated cutting and becomes dominant. Thus the sere is not only stopped in its normal progress to scrub and woodland but is deflected to form a new climax.

Again, when a wood is coppiced, i.e. cut to the stumps, most of the trees and shrubs shoot from the stools and in a few years coppice vegetation is established. If it is now left alone the coppice gradually becomes "overgrown," very tall and dense. Ultimately, however, trees will grow up above the height attained by the coppiced shrubs and will gradually come to dominate the wood, shading the shrubs as they did originally. This process is an example of a subsere. If, however, the coppice is again cut and the coppicing is repeated every ten or twelve years, as in the old normal practice, the succession to high forest is permanently prevented and a cycle of vegetation is established corresponding with the coppicing period, and depending on the gradual growth of the coppice till it is cut again. The sparsely developed field layer under old coppice is stimulated by the sudden access of light, and the woodland plants start to grow more actively, and to flower profusely, so that in the second, third, and fourth years after coppicing the ground may be covered with a floral carpet. At the same time plants alien to the woodland flora very often intrude. Woodmen, shooters, and others bring in seeds from outside on their clothes and boots, and the open soil between the sparse woodland plants gives the opportunity for these aliens to germinate and establish themselves in the coppice. As the shrubs grow up again and the ground becomes more and more deeply shaded, the flowering of the woodland plants diminishes and their growth slackens, while the aliens, which are usually plants demanding full illumination, are often exterminated, though their seeds may lie dormant in the soil for many years and germinate to produce new plants when the wood is again cleared. Thus the regular practice of periodic coppicing imposes on

the woodland vegetation a cyclic development showing a characteristic succession within each coppicing cycle.

Another case is the pasturing of developing chalk grassland. Bare chalk soil is colonised by a variety of plants, prominent among which are a number of species characteristic of the chalk down pastures. If left to itself this vegetation is soon invaded by the seedlings of shrubs and trees, provided there are enough seed parents in the neighbourhood, and chalk scrub and ultimately beechwood are developed. That would be a normal prisere. But if the vegetation is regularly pastured the woody seedlings cannot make headway and grassland with a close turf is established, dominated by the fine-leaved fescues (*Festuca ovina* and *F. rubra*) with which a number of other herbs are constantly associated. This very characteristic plant community forms no part of the normal prisere but is a climax vegetation resulting from continuous grazing and thus deflected from the early stages of the prisere. Any vegetation which is stable under conditions to which it is continuously subjected may be counted as a climax, whether the conditions are those of climate and soil alone, or whether they include a man-made factor such as grazing, periodic burning (as on many heaths and moors), or regular periodic mowing of fen or meadow, or coppicing of woodland. Thus we may distinguish climatic, edaphic (soil), and anthropogenic climaxes.

The existing vegetation of a country like England is therefore a mosaic whose constituent pieces are plant communities of the most varied status. First there are the natural climaxes which would be substantially what they are whether man were present or not. Among these are the few fragments of untouched or almost untouched native woodland. To them may be added the much more numerous woods that are substantially natural woods from which timber is sometimes taken, and which are found mainly in the north and west. Other pieces of natural climax vegetation are seen in the grassland, heaths, moors, and bogs which lie above the limit of forest-growth; others again in the distinctive climate and on the distinctive soils of the higher mountains; in a few pieces of fen which have

been allowed to progress to fen woodland; and in certain sea-coast vegetation.

Then there are various seral stages, vegetation which is demonstrably undergoing automatic successional progress towards a natural climax. These may be found in any of the localities where the natural climaxes would occur, especially where new soil is often exposed by natural agencies, but except in remote regions they are rarely left undisturbed by man's activities.

Far commoner than natural climaxes or priseral stages are semi-natural communities resulting in one way or another from human action. Much the greatest area of these is the grassland used for pasture, of which the "rough grazings," which owe nothing to seed mixtures or manure, are the nearest to strictly natural vegetation. They are mostly situated on hillsides and have come in place of forest through the effect of pasturing, though in many cases the original forest had been previously cleared. The deflected succession resulting from the grazing and trampling of sheep or cattle has been stabilised in turf-forming communities dominated by grasses. So long as the grazing regime remains constant these will remain substantially unaltered. But undergrazing, overgrazing, the substitution of sheep for cattle, or vice versa, or even change in the time of year during which the pastures are grazed, will at once lead to change. Besides the rough grasslands proper, much of the heath, moor, and even bog, which covers the hillsides and plateaux of the north and west, and also many of the lowland heaths, are modified, i.e. deflected from normal succession, to a greater or less degree by grazing and also by burning. Seral stages between the modified forms of any of these types of vegetation and between these and the natural climaxes are very common indeed and require prolonged observation and study before they can be "sorted out" and the status of the numerous communities properly determined.

The "permanent grass" fields, which occupy about half the English lowlands and considerable areas in Wales, differ from the rough grazings because they are enclosed and often manured. Frequently, too, they have been originally "laid down to grass," i.e. sown with grass seed

on arable land. Thus they are very much less "natural" than the rough grazings, but nevertheless they must be counted as "semi-natural" plant communities because they consist entirely of native grasses and herbs and, since they remain in existence for a long time, they behave in many respects like a natural community. Like the rough grazings, their composition rapidly changes with alterations in the grazing regime, and also, of course, with changes in manuring. Under a constant regime the permanent grass communities attain considerable stability.

The poor condition and semi-derelict state of a very great deal of our permanent grass had long been one of the major scandals of British agriculture. The failure to maintain a proper grazing regime, neglect of manuring, neglect of drainage on waterlogged land, had led to serious and widespread deterioration and the establishment of plant communities of almost worthless grasses and herbs. When the land will not carry its proper complement of stock serious undergrazing results, and then the pastures are invaded by shrubs, or in other words a subsere is initiated which would ultimately lead to woodland. This is the type of land which has been extensively ploughed, properly cultivated, and used for arable crops during the late war.

Much of what is called "waste land," such as is found on many of our lowland commons, shows a complex mixture of grassland, heath, scrub, and even fragments of woodland. It is generally intermittently and casually pastured, and local fires often temporarily destroy considerable areas of the vegetation. The grassland and heath owe their existence to grazing, trampling, and burning, but shrubs and trees are always trying to invade it and to establish scrub and woodland. In other words, subseres leading to a woodland climax are always starting but are constantly destroyed by woodcutting, by a renewal of pasturing, or by burning. The result is a chaotic mixture of temporarily stabilised plant communities with stages of subseres.

Finally, we come to the purely artificial plant communities such as plantations of alien trees and arable crops. By far the commonest plantations are of conifers not native to this country and apart from larch and spruce they come largely from north-western America: these the Forestry

Commission is now using on a large scale. Most of these trees are evergreen and cast so deep a shade when closely planted that little or no vegetation can exist beneath them. Their fallen leaves or branchlets form an acid raw humus which also tends to make the soil unsuitable for most woodland plants, and often leads to definite deterioration. It is too early to say what will be the fate of most of these plantations. The larches, however, both the European and the Japanese larch, which are also very commonly planted, have soft and deciduous foliage, and when a plantation is made on the site of an old deciduous wood the undergrowth is often apparently not very greatly changed, though we have little exact knowledge of what actually occurs.

Arable crops have a special status. They are artificial communities whose "dominants" are the crop plants, while the "associated species" are the arable weeds, i.e. the native plants which come unsought into the community and whose competition sometimes seriously interferes with the growth of the crop, even to the extent of impairing its dominance. Various means are taken to combat the more harmful weeds, ranging from simple hoeing between the rows of plants of a root crop to arranging to cultivate a sequence of crops in the same field which minimises the possibilities of luxuriant weed-growth. Many of the small annual weeds, however, are not only impossible to exclude but actually do little harm to the crops. Owing to the fact that these communities are composed of artificial dominants and associated plants which may compete with them, and also to the very short life of the community, ranging from a few months to two years at the most, the problems of their economy as examples of vegetation are very different from those of natural and semi-natural plant communities, and they have in fact been very little studied except for the purely practical purposes of agriculture.

CHAPTER VI

THE BRITISH OAKWOODS

That oak forest is the natural vegetation of the more favourable soils over most of Great Britain was made plain in our first two chapters. There is good historical and prehistorical evidence that from middle post-glacial times it extended throughout the country except where altitude or soil conditions were definitely unfavourable. In the Highlands it occupied the valleys and the lowest slopes of the hills where the soil was relatively good, giving way to birch and pine at somewhat higher levels, on poorer soils, and in the extreme north. In Ireland the principal oakwoods, remains of which still exist, were in the valleys of the siliceous mountains of the coastal regions both in the east and in the west.

This British and Irish oak forest represented the extreme north-western portion of the western and central European deciduous forest, considerable parts of which are still dominated by oak. The other leading dominant of the continental forests is beech, and certain southern English woods, mainly on chalk soils, are beechwoods. But oakwood, since Boreal times, has always been, and still is, by far the commonest type of natural and semi-natural deciduous British woodland.

In early historical times and throughout the Middle Ages down to the beginning of the modern period many great forests remained, though most of the country was increasingly farmed, local woods being retained for the supply of timber and small wood. To mention only some of the more important of these great forests in the south and midlands, there were large parts of Anderida, which in Roman times had extended westward through the Weald from the borders of Kent and Sussex to the Hampshire uplands; Windsor Forest; the Forest of Essex; the Forest of Arden in Warwickshire; Wychwood in Oxfordshire; the Forest of Dean in Monmouthshire; Wyre Forest in Worcestershire; Sherwood Forest in Nottinghamshire; and all

these were oak forests. It was under the oaks of Arden that Shakespeare's exiled duke held sylvan court, and it was among the oaks of Sherwood that Robin Hood hunted the deer and held up the wealthy Nottingham burgesses.

But the need of wood and the claims of grazing and tillage gradually ousted the hunting interests for which the Normans had reserved the Royal Forests and the Chases,[1] while increasing grazing in the forests themselves and excessive felling of trees degraded or destroyed more and more of the old woodlands. Even those areas which were left under trees were so heavily robbed of sound timber that in the seventeenth century most of the remaining oaks of any size were old and decayed, the vigorous younger trees having been removed and the seedlings destroyed by grazing animals. Almost the only form of oakwood that was well maintained in the south and in the midlands came to be oak-hazel coppice-with-standards, which for several centuries played an essential part in rural economy. Later on the standard oaks were neglected and the coppice remained the only useful element, so that many old oak-hazel woods came to be represented by coppice alone. To-day even this is of very restricted value and is often allowed to become overgrown, though a good deal still remains as fox covert and pheasant preserve and much of the coppice is still regularly cut. Well-grown high oak forest is rare in the south-east and midlands and most of what little there is has probably been planted, as indeed have many of the oak-hazel woods, though nearly always on the sites of old oakwoods. But by comparing the flora of oakwoods of every kind still remaining we can arrive at a very fair notion of the natural composition of oakwood vegetation.

There are two native British species of oak—the pedunculate or common oak (*Quercus robur*) and the sessile-fruited or durmast oak (*Quercus sessiliflora*), though they are closely similar trees and not distinguished by the non-expert. The former bears its acorns on long slender stalks, while its leaves are sessile or with very short stalks, and at the base of the blade adjoining the stalk there is on each side a tiny crescentic fold ("auricle") of leaf

[1] The Chases were hunting forests reserved for landed nobles and were usually smaller than the Royal Forests.

tissue. The underside of the blade is smooth. The acorns of the latter have no stalks or sometimes short thick stalks, while the leaves have fairly long stalks into which the base of the blade gradually tapers. The lobing of the leaf is usually shallower and more regular than in the pedunculate oak, and the underside of the blade bears branched, usually star-shaped hairs, either a few large ones along the sides of the veins or smaller ones covering the surface more or less completely. The two species, however, hybridise freely when they live close to one another, so that many oaks show a mixture of these two sets of characters. But where either species occurs pure in large areas the characters given are remarkably constant in every tree one examines.

The pedunculate oak is the regular woodland and hedgerow tree of midland, south-eastern, and most of southern England (Phots. 3, 7, 8), and one may travel far in these regions without seeing a single sessile oak. In the siliceous (i.e. non-calcareous) hill and mountain regions of the west and north of England and Wales and on the similar hillsides of Ireland, on the other hand, practically all the woods are composed of sessile oaks (Phots. 4, 5, 6). But sessile oaks are by no means absent from the east and south-east of England. On sandy and other acid soils they are often found, either alone or in company with the pedunculate oak, and here naturally we also meet with many hybrids. Sessile oaks rarely grow naturally on neutral or alkaline soils, but pedunculate oaks do grow on acid soils. Not only are pedunculate oaks common, and sometimes dominant, on the acid sands of the south-east, but some fragments of completely natural oakwood on the granite of Dartmoor (Phot. 15, p. 92) and in Cornwall are entirely composed of them. On the plains and valley bottoms of the west and north, also, i.e. where the rocks are softer and the soil deeper, the pedunculate oak is the characteristic tree.

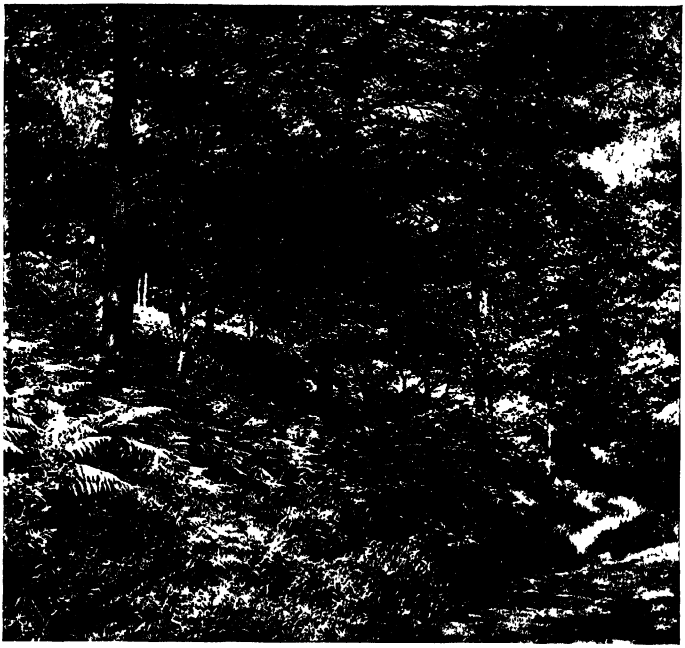
Planting of oaks has been very widespread for two or three centuries and both species have been planted, the pedunculate oak apparently in much greater number, and this has of course confused the natural distribution of the two species, and increased the number of hybrids. In

A. G. T.

PHOT. 3. Oakwood in close canopy. Trees (pedunculate oaks) about 30 years old. This wood is said to be a direct descendant of the original oak forest of the Weald. Staffhurst Wood, Surrey, April.

R. J. Lythgoe

PHOT. 4. Oakwood of durmast oaks in close canopy with no shrubs. Trees perhaps 60 years old. Field layer of bracken and bilberry. Valley in the Quantock Hills, Somerset, September.



W. B. Crump

PHOT. 5. Durmast oakwood on a Pennine valley side. Rather open, but few shrubs. Bracken and wood soft-grass.

W. B. Crump

PHOT. 6. Upland durmast oakwood near the tree limit. Oaks poorly grown. No shrubs. Bilberry and wavy hair-grass.

Scotland particularly there is a great mixture of forms, so that in many woods it is difficult to find a typical tree of either species, and this is probably largely due to the extensive eighteenth and nineteenth century planting and subsequent crossing. While we should expect the sessile oak to be the native species in most of the glens, it is probable that the pedunculate oak is native round the sheltered bays and inlets on both east and west coasts of northern Scotland. In spite of these mixtures and confusions, the general principle that the pedunculate oak is the native tree on the clays and loams of the English midlands, east, and south, and the sessile oak on the acid siliceous rocks of the north and west, is perfectly good.

In Europe the pedunculate oak goes farther north and much farther east than the sessile, and thus seems to be better adapted to the continental climate. This may be connected with the fact that the sessile oak is the characteristic tree of the western parts of the British Isles, while the pedunculate species is apparently absent from the extremely oceanic climate of western Ireland—perhaps, as a native tree, from the whole of Ireland. Of trees other than oaks commonly found in oakwoods, wych elm and ash nearly rival the oak in potential height, all three being able to attain well over 100 feet when grown in close canopy on good deep soil.

OAKWOOD TREES

The wych elm (*Ulmus glabra*, better known as *Ulmus montana*) is a magnificent, lofty, wide-spreading tree with a great dome-shaped crown when it is well grown in the open. It is distinguished from the other British elms (which rarely play any part in our existing woodlands) by its large rough leaves,[1] broadest above the middle (obovate), coarsely toothed, and with a terminal cusp. Some of the leaves on almost every tree have three cusps, one on each side of the apical cusp. Like all our elms, it flowers very early (February or March) and ripens its fruits in April. The dry fruit has a single flattish central seed

[1] The name *glabra* refers to the smoothness of the *fruits*.

surrounded by a wide membranous margin so that it is easily carried by the wind.

The wych elm is scattered through the southern English oakwoods, but is much commoner in the west and north, where it is specially frequent in the limestone ashwoods. It is frequently cut with the coppice and makes strong shoots from the stools, but does not sucker from the roots like most of the other elms. Judging from the pollen in prehistoric peats some kinds of elm, which may have been wych elm and perhaps other species, were very much more abundant in the south of England in some earlier post-glacial times than they are now.

The ash (*Fraxinus excelsior*) is one of the commonest and also one of the finest of British trees, and its loose light green foliage, ribbed grey bark, and bunches of winged fruits ("keys") are very familiar. The leaves are compound (pinnate), with the several pairs of narrow leaflets arranged along the leaf stalk. The ash produces bunches of small inconspicuous flowers in early spring, and the abundant fruits are carried about by the wind in great numbers, the seedlings often springing up in masses.

The ash forms pure woods on shallow limestone soil (Chapter VIII, p. 116), where oaks do not flourish, but is also common in oakwood on good soil, avoiding poor sandy ground. It is favoured both by highly calcareous and also by wet soils. Thus it is common in oakwoods which are wet and in regions of high rainfall: also in those on *deep* soils derived from limestone and on calcareous clays such as the chalky boulder-clays of south Cambridgeshire and adjoining counties. In these last it is coppiced along with hazel and other shrubs, the oaks being left as standard trees. These woods may be called (ash-) oak-hazel woods (see p. 86).

Field maple (*Acer campestre*) is a very common tree of the southern English oakwoods, but it is nearly always coppiced. When allowed to grow up from the seedling to maturity it makes a handsome dome-shaped tree of moderate height with rather dense compact dark green foliage. The fruit, as in all maples, is double, splitting when ripe into two one-seeded halves. The membranous wings stand out laterally so that they form a straight line before the

R. J. Lythgoe

PHOT. 7. Edge of pedunculate oakwood with dense coppice of hornbeam (centre and right) and hazel (left). Near Burwash, E. Sussex.

The Times

PHOT. 8. Pedunculate oakwood grown in close canopy but recently thinned. Sparse shrub layer of hazel and sallow. Carpet of wood anemones. Sussex. April.

Face p. 72

halves split apart. In the sycamore (*Acer pseudo-platanus*), which is a bigger and loftier tree than field maple and has much larger leaves, the wings of the fruit are bent so that they make an angle or even run parallel. Sycamore is not a native of Britain though it is a common constituent of the deciduous forests of central and southern continental Europe. The earliest records of planting in England date from the sixteenth century and it has been extensively planted throughout Britain during the last two centuries, being a quick-growing wind-resistant tree whose wood is useful for several purposes. It sows itself very freely and has become a self-sown constituent of many semi-natural woods. The old leaves are often disfigured by black blotches produced by the fungus *Rhytisma acerinum*.

Hornbeam (*Carpinus betulus*) is associated with oak in a restricted area of south-eastern England—Kent, East Sussex, Essex, Middlesex, and Hertfordshire—with some slight extension into adjoining counties. It also appears to be native near Bristol and near Chepstow in the west, but not elsewhere in Britain. It is nearly always coppiced, and over much of its area it replaces hazel (or is mixed with hazel) as the dominant coppice layer of oakwood (Phot. 7). Since it is very tolerant of repeated cutting, hornbeam has been much used for hedges and arbours. When allowed to develop it makes a graceful tree of moderate height. The wood of hornbeam is very hard and was formerly used for many purposes for which metal is now employed. Like beech, the tree was apparently a late post-glacial immigrant.

Alder (*Alnus glutinosa*) grows in wet depressions in oakwoods and along the sides of brooks or ditches running through the woods. It is dominant on marshy ground and forms almost pure woods in undrained fenland (see p. 120). In the wet western climates of Wales and western Scotland alder is very frequent in many of the sessile oakwoods of the hillsides, not necessarily on marshy ground. It was far commoner in the wet Atlantic period and throughout the Sub-Atlantic and early historical times than it is now, since most of its wet habitats have been drained. Its charcoal was extensively used in the manufacture of black

gunpowder, and plantations of alder by stream-sides may still be met with.

Of other catkin-bearing trees (*Amentiferae*)—to which group nearly all the dominant trees of our woodlands, oak, beech, birch, alder, as well as hornbeam and hazel, belong—occurring in oakwood the birches and poplars must be mentioned here. Two native species of birch—the silver birch (*Betula pendula*), with whiter bark and often pendulous branches, and the hairy birch (*Betula pubescens*)—are commonly met with in oakwood; and in open oakwood on sandy soil either or both may be very abundant, sowing themselves freely and filling up gaps in the wood, as for example at Burnham Beeches and in numerous woods on the sands of the Weald and other sandy soils of south-east England. But the birches are light-demanding trees and cannot survive in close oakwood. They produce abundant seed, and the very small and very light, one-seeded, winged fruits are easily scattered in great quantity by the wind, the seedlings often springing up in masses on open sandy tracts of ground. Aspen (*Populus tremula*) is also a light-demanding tree, of no great size, which inhabits a considerable variety of soils, and, like the birches, often occurs in open oakwoods. Its leaves are almost circular in outline, coarsely toothed, and smooth. Aspen suckers freely from the roots and thus forms small thickets. The foliage of both birch and aspen is loose and light, so that it does not shade the ground at all deeply. The grey poplar (*Populus canescens*), with coarsely toothed leaves, covered beneath when young with a grey or white down, is much less common but is sometimes seen in rather wet oakwoods in the south and east, for example on the Weald clays and in East Anglia. The white poplar (*Populus alba*), with lobed maple-like leaves, glistening white below, is not a native, though often planted. The black poplar (*Populus nigra*), with dark green, finely toothed leaves, the branches massive and arching, usually bearing large bosses, is very local as a native tree. It is quite rare in oakwood, but fine examples occur as isolated trees, for example by the side of the River Lark in Breckland. The Lombardy Poplar (*Populus italica*) is of course the most familiar poplar, because of its striking shape, like a furled umbrella. It is

not a native tree, but is very widely planted, and its tall spires have become conspicuous features in many English landscapes. The black Italian poplar (*Populus serotina*), a tall tree with fan-like crown, is a hybrid, and is one of the most widely planted trees in Britain.

Willows belong to the same family as poplars, but willow trees, as distinct from shrubs (e.g. the sallows, see p. 77), are scarcely natural constituents of oakwoods.

There are several trees belonging to the rose family (*Rosaceae*) which often grow in oakwoods. Of these the wild cherry or gean (*Prunus avium*) is one of the largest, and is conspicuous in April by its abundant gay clusters of white flowers which produce quite inedible "cherries." Bird cherry (*Prunus padus*), with smaller flowers in racemes,[1] not clusters, is not wild in the south of England, but is frequent in both oak and ash woods in the north. The true cherry (*Prunus cerasus*) is very occasionally seen in southern oakwoods, where it is probably native.

The crab apple (*Malus communis*), a smaller tree than the cherries, with pink and white petals, is quite frequent in oakwoods. Unlike the pear, which, when growing wild, is probably always an escape from cultivation, the apple is a true native of Britain. Allied to the apple and pear are the trees belonging to the genus *Sorbus* with compound inflorescences and much smaller fruits. Mountain ash or rowan (*Sorbus aucuparia*) is the most frequent. It is distinguished by its pinnate leaves with serrated leaflets, clusters of small white flowers (June) and bright red, berry-like fruits (September). Mountain ash is occasionally, though not very commonly, seen in south-eastern oakwoods. In the northern and western hill country it is more frequent, and in the Scottish Highlands is one of the commonest trees, ascending higher on the mountains than any other. In Wistman's Wood on Dartmoor it is the only tree accompanying the oaks. The wild service tree (*Sorbus torminalis*), whose broad leaves have sharply cut triangular lobes, is scattered rather sparsely through the southern oakwoods, but in some localities is abundant. It makes a fine tree but is usually cut with the coppice. The

[1] In a *raceme* the main stalk (peduncle) of the inflorescence has secondary stalks (pedicels), each bearing a flower, arranged along it at intervals.

whitebeam (*Sorbus aria*) is rarely an oakwood tree (see pp. 99, 112).

Two evergreen trees remain to be mentioned. Holly (*Ilex aquifolium*) is by far the commonest native British evergreen, except the climbing ivy, and is abundant in many oakwoods where it has not been cut out. It specially enjoys the damp mild climate of the south-west. In the oakwoods of Killarney (p. 90, and Phots. 13, 14) in south-west Ireland holly forms a continuous under-storey below the oaks. Single trees of yew (*Taxus baccata*), one of the three native British conifers (pine, yew and juniper),[1] are occasionally seen in oakwoods, though they are much more abundant in beechwood and in chalk scrub (see pp. 99, 112).

OAKWOOD SHRUBS

Hazel (*Corylus avellana*) is the commonest oakwood shrub, and in the typical coppice-with-standards the coppice is very often almost pure hazel. Even in planted hazel coppice, however, other shrubs are usually found, having got in by themselves. Hazel generally grows as a shrub, producing multiple stems from the base, a habit much encouraged by coppicing. When it is not cut for twenty years or more it may reach a height of 20-25 feet and then casts a deep shade on the floor of the wood. The coppice wood is useful for a variety of purposes—hurdles, fencing, pea and bean sticks, etc. The decrease in the practice of folding sheep has led to a lessened demand for hurdles and thus to the neglect of coppice.

Hawthorn (*Crataegus monogyna*) is another very common oakwood shrub, often found in the woods. It has of course been almost universally used for "quick" hedges throughout the English lowlands, and this has led to an enormous increase in the number of hawthorn bushes in the country. When a quick hedge is neglected and grows tall it flowers abundantly, giving brilliant shows of "may" in a favourable year. It also fruits abundantly and the seed from the "haws," distributed by birds, is very widely scattered, so

[1] Neither yew nor juniper bear dry cones like the pines, larches, firs, cedars, etc. They both have succulent berry-like fruits, but they are nevertheless clearly allied to the ordinary conifers.

that hawthorns appear almost everywhere in suitable situations, including more or less open oakwoods. Grown in shade its foliage is sparse and it does not flower. In Scotland, where quick hedges are not in general use, the shrub is far from common, not because it cannot grow there but because the supply of seed is very much less. Many of the shoots of hawthorn are arrested in growth and become sharply pointed spines; and when cut back, it does not form long quickly growing shoots like hazel and many other trees and shrubs, so that it is never a proper constituent of coppice. When allowed to grow freely, hawthorn, like hazel, attains a height of 25 feet, or even more, and has the form of a small tree.

Blackthorn or sloe (*Prunus spinosa*) is another spinose shrub commonly found on the edges of oakwoods and on waysides. It is markedly gregarious in habit, suckering freely from the roots, and produces masses of white blossom in April. The highly astringent black sloes ripen in September, but in some years the crop is very poor owing to April frosts. A flowering sloe is in the centre of Phot. 3.

Among the other abundant shrubs of oakwood are the sallows, which are shrubby species of willow (*Salix*) and bear their male and female flowers on separate bushes. Of these the common or grey sallow (*Salix atrocinerea*) is the commonest and is locally abundant in or on the edges of damp oakwoods, where it is cut with the coppice. The leaves are three times longer than broad, and the buds hairy and blackish. The goat willow or great sallow (*Salix caprea*) has broader leaves and smooth yellow buds. Branches of both sallows, bearing male catkins with their bright yellow anthers, are called "palm," and are used to decorate churches on Palm Sunday. The young ovaries of the female catkins are green, and develop into capsules which contain minute seeds distributed by the wind with the aid of a pencil of silky hairs attached to each. Sallows grow in marshes and fens as well as in oakwoods, and the grey sallow is an exceedingly common plant with a wide range of habitats. The goat willow may also be found in quite dry copses on chalky soil. A lower-growing sallow (*Salix aurita*) with smaller, wrinkled leaves is sometimes found in southern oakwoods on acid soils, but is much

commoner in the Highlands and in western Ireland. The Latin name *aurita* (eared) refers to the large conspicuous stipules (wings at the base of the leaf). Shrubby species of willow other than the sallows, such as the common and purple osiers (*Salix viminalis* and *purpurea*) with very long narrow leaves, are scarcely oakwood shrub, though they may be found, wild or planted for their "withies" used in basket-making, on wet margins or by the sides of streams.

Guelder rose (*Viburnum opulus*) is a shrub frequent in damp oakwoods and coppices well. It has lobed, rather maple-like, leaves and flat inflorescences, whose outermost sterile flowers have large white expanded corollas. In the cultivated guelder rose or "snowball tree" (variety *sterilis*), planted in gardens, the inflorescence is globular and consists entirely of these sterile flowers. The fruits of the wild guelder rose are red, translucent, and very soft.

Various other shrubs may be found in oakwoods whose soil is rich in lime or other basic salts. The commonest of these is perhaps dogwood (*Cornus sanguinea*) with its purplish leaves and shoots, deepening in colour in autumn. Other less common kinds are spindle tree (*Euonymus europaeus*), whose rigid wood was at one time used to make spindles and skewers and whose beautiful pink fruits open to show the deep orange seed-covering (*aril*); privet (*Ligustrum vulgare*); elder (*Sambucus nigra*); common buckthorn (*Rhamnus catharticus*), a somewhat spiny shrub with finely serrated leaves. All these are much more abundant on calcareous soil (see p. 86). The alder-buckthorn (*Frangula alnus*), on the other hand, grows mainly on damp acid soils and is locally abundant in oakwoods and on damp heaths. It is not at all spiny, and its wood, which is very brittle, was formerly used, like that of the alder, for making the charcoal used in the old black gunpowder. The dark shining leaves are broadest above the middle.

Two other kinds of shrub-like plants stand rather apart from those already described. These are the ubiquitous prickly wild roses or briars (*Rosa*), and brambles (*Rubus*), of which various species are among the commonest plants of oakwoods and their edges. On the floor of a wood the brambles sometimes form a continuous low growth about

two feet high and are to be counted as belonging to the "field layer," usually consisting of herbs, rather than to the shrub layer. In this deeply shaded position the brambles do not flower. In many exploited oakwoods and oak-hazel woods throughout their range (and in beechwoods too) the brambles are most troublesome weeds. They form long arching shoots, often scrambling over the shrubs with the help of their strong curved prickles. When the tips of the shoots reach the ground they strike root, forming points from which new shoots spring, thus producing an ever-extending tangled mass of prickly vegetation which excludes many of the woodland plants; though a few, such as bracken and honeysuckle, can grow through the tangle. To maintain the varied woodland flora and enable tree seedlings to establish themselves and regenerate the wood, the brambles should be drastically and continuously cut out. The numerous species of bramble are very much alike and difficult for the non-expert to distinguish. They were originally lumped together as one species (*Rubus fruticosus*). An easily recognisable species is the dewberry (*Rubus caesius*), a low-growing, creeping plant with much less formidable prickles. Wild raspberry (*Rubus idaeus*) is also found locally in oakwoods.

The two commonest wild roses are the common dog-rose (*Rosa canina*) and the "field rose" (*Rosa arvensis*) with white flowers. Unlike the brambles, the wild roses can stand erect, though their stems are weak. Their flowers open in June, before those of the brambles. The scarlet "hips" of the roses and the "blackberries" of the brambles, together with the "haws" of hawthorn (none of which are produced under the deep shade of woods), are of course the most familiar fruits of hedges and the borders of woods in the autumnal countryside.

Besides the trees and shrubs two woody climbers, the evergreen ivy (*Hedera helix*) and the honeysuckle (*Lonicera periclymenum*), are very common in oakwoods. Ivy climbs by means of adhesive roots and thus needs a broad surface to climb on, such as a rock or the trunk of a tree. In many woods practically every tree is covered with ivy. Foresters destroy it by cutting through the main stem near the base, for it damages the growth of trees by preventing necessary

gas exchange through the bark and sometimes by smothering and breaking down branches. If ivy cannot find a suitable tree trunk to climb it creeps on the ground, rooting at intervals and often covering considerable parts of the floor of a wood. Honeysuckle twines round any thin erect object it can find, and its twisted stems, which may be quite thick, often hang down in loops or festoons, like a tropical "liane," from the branches of shrubs or trees. If it cannot find anything to climb on, honeysuckle, like ivy, creeps on the ground, rooting as it goes.

STRUCTURE OF OAKWOOD

An oak-hazel wood (coppice-with-standards) is a semi-natural wood brought into existence by human agency, whether actually planted or not, but it serves very well to illustrate the *structure* of woodland. The tree layer of standard oaks in "open canopy" is seldom more than 50 or 60 feet high, though oaks can attain a height of well over 100 feet when grown in close canopy. The tree canopy is underlain by the *shrub layer* (coppice), which seldom exceeds 8 or 10 feet in height if it is regularly cut every ten or twelve years. Below this comes the *field layer* of herbaceous plants, and close to the soil a *ground layer* consisting chiefly of mosses. These four layers are typical for British woods of all kinds, but in many woods one or more of the lower layers may be nearly or quite absent.

In a young natural oakwood or in a plantation where the saplings are closely set and cast a deep shade, scarcely any vegetation grows below them, but in an older wood which has been thinned or in which all the weaker saplings have been shaded out and killed, but which is still in close canopy, shrubs, herbs, and mosses will have colonised the wood, establishing the three lower layers. As the canopy "opens out," i.e. bears less dense foliage, with the growth in length of the branches and the dying off of lower ones so that more light is admitted to the lower layers of the wood, the shrubs and herbs increase in luxuriance, though neither forms a continuous sheet of vegetation. If one layer is locally dense, those below are sparse or absent. Thus a thick shrub layer casting deep shade,

as in old coppice, tends to cut out, or at least diminish, the field layer, and a very dense layer of herbs prevents the growth of mosses. All four layers are most fully represented where the tree layer lets through most light and the shrubs are regularly cut, as in the coppiced oak-hazel wood with standard oaks in open canopy. Here the field layer is particularly well developed, almost completely covering the ground in the second and third years after coppicing. When the coppice grows up and casts deep shade towards the end of the cycle the field layer plants become sparse and feeble and most of them cease to flower; but many remain alive, vegetating weakly, and resume vigorous growth as soon as the coppice is cut and light again admitted.

The tree and shrub layer of a coppice-with-standards may consist almost entirely of oak and hazel respectively, but even a planted wood is normally invaded by other trees and shrubs. Of trees, ash, field maple, locally sycamore, wych elm, birch, aspen, and gean are among the commonest, and all of these are very often coppiced so that they figure in the shrub layer. Of shrubs proper, hawthorn, blackthorn, and sallows are nearly always present, and of other kinds, apart from roses and brambles, which are everywhere abundant, dogwood and guelder rose are perhaps the most frequent, especially on good fertile soils. In high forest the number of individual shrubs is much less and a continuous shrub layer is rarely formed. In many of the sessile oakwoods on the northern and western hillsides shrubs are very few indeed (Phot. 5), and towards the upper limits of altitude they may be absent altogether (Phot. 6).

Many oakwoods are more or less derelict owing to maltreatment—indiscriminate felling, invasion by cattle, excessive trampling, or infestation by rabbits or voles—and in these the trees are sparse and often ill-grown, the shrub layer is irregular, and "weeds" are numerous. On common land or waste ground, and even in enclosures, fragments of such woods are often seen, with a few trees here and there, interspersed with shrub thickets and patches of grass and herbs. But it is easy to see from the general character of the flora—poor though it often is—that such areas are

degenerate oakwoods, though some of the herbaceous species are "weeds," i.e. they are alien to the woodland flora.

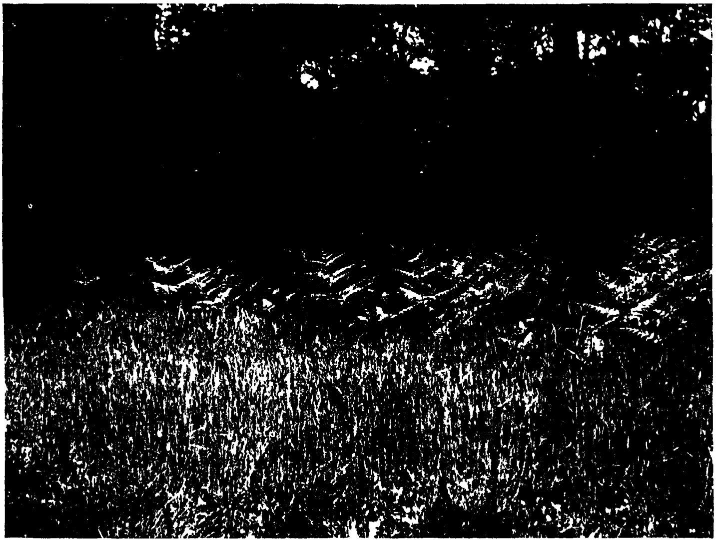
THE FIELD LAYER

The field layer of oakwood differs according to the particular soil on which the wood is growing. On the poor sands, acid in reaction, where the oaks are usually poorly developed, the field layer is heathy and *mor* tends to be formed on the surface (see p. 89). The field layer is largely determined by the amount of water held in the soil.

On the lighter and drier soils the common bracken fern (*Pteridium aquilinum*) often dominates the field layer (Phots. 9, 10); it cannot grow in waterlogged soil, and is most luxuriant on sands and similar light soils. In open oakwood, where a great deal of light penetrates, or on quite open ground, the tough leathery bracken fronds grow obliquely upwards, and are set so close together and shade the ground so deeply after they are fully expanded in June that nothing can grow beneath them. This is partly because of lack of light and partly because the soil is covered by a thick layer of bracken litter, consisting of an accumulation of fragments of dead fronds passing down into raw humus. Where there is a continuous tree canopy but still sufficient light for the dominance of bracken the fronds are much less numerous and bend over into a horizontal position, while their substance is softer and thinner. Here the bracken litter is no longer preponderant, the humus is of the *mull* type (see p. 35), largely derived from the leaves of the oaks, and numerous other woodland plants are present.

In many south English woods on dry soil bracken is associated with dominance of bramble (*Rubus fruticosus*, see p. 79). The "fiddle heads" of the bracken push up in May through the tangle of bramble shoots and expand their fronds above. Owing to the dense mass of vegetation formed by these two plants few other species are present, but honeysuckle (*Lonicera periclymenum*) is a frequent associate.

One of the commonest associates of bracken in oakwoods on light and rather poor but not excessively acid "heathy"



C. G. P. Laidlaw

PHOT. 9. Edge of durmast oakwood in close canopy. Bracken and wood soft-grass. Forest of Dean. June.

C. G. P. Laidlaw

PHOT. 10. Bluebells in flower and young bracken fronds in durmast oakwood. May.

Face p. 83.

soils throughout the country is the wood soft-grass (*Holcus mollis*). This grass vegetates during April, May, and early June before the bracken fronds are fully expanded to form their dense canopy (Phot. 9). The roots of *Holcus* occupy the surface layer of soil and thus do not compete with those of the bracken, which spring from the rhizomes at a greater depth. Another plant which often accompanies either or both of these two is the bluebell or wild hyacinth (*Scilla non-scripta*, Phot. 10). This forms bulbs, often at a depth of 8 or 10 inches, from which the shoots begin to grow in winter, appearing above the soil in February or March and flowering in April and May (often earlier in the south-west and later in Scotland). Thus the bluebell does most of its vegetative growth before the soft-grass, and this before the bracken, and since their roots occupy different layers of soil, they can grow together without serious competition. In woods on light soil the bluebell often grows very thickly, producing the well-known sheets of deep blue fragrant flowers. The bluebell often picks out and densely covers islands of sandy loam in the middle of tracts of clay (for example, on the plateau of the Chiltern Hills in Bucks and Oxon), while it is scarce or absent on the surrounding heavy soil. Wood violet (*Viola riviniana*), wood sage (*Teucrium scorodonia*), tormentil (*Potentilla erecta*), barren strawberry (*Potentilla sterilis*), and wood anemone (*Anemone nemorosa*) are frequent members of the soft-grass-bracken community.

Wood anemone flowers in March and April and the foliage disappears in June. It is one of the commonest plants of our oakwoods, growing on a wide range of soils from sands to clays and starring the floors of the oakwoods in early spring with its elegant white flowers, so that at this season it is often a real dominant of the field layer (Phot. 8). Lesser celandine (*Ficaria verna*) is another very common woodland plant of early spring, developing in February and flowering in March and April, while its leaves disappear in June, even earlier than those of wood anemone. Its bright yellow, eight-pointed, star-like flowers appear everywhere on waysides and hedgebanks as well as in woods on similar soils, but it does not cover such wide areas of woodland as the anemone.

The more fertile soils, which are generally loams, with a wide range of texture, adequate moisture, and rich in nutritive mineral elements, bear the richest and what may be called the "central" types of oakwood, contrasting with the drier types just described on one side and the wet oakwoods on the other. One of the best known and most abundant plants of the field layer is the primrose (*Primula vulgaris*). The pale yellow, faintly but deliciously scented flowers are at their best in April, though in sheltered situations, particularly in the mild south-western climate, they begin to appear much earlier, sometimes in mid-winter. Primrose is especially a plant of clays and loams, though it grows on almost any good soil, avoiding coarse sterile sands and shallow calcareous soils. It is often freely mixed with anemone, wood violet, or sanicle, but sometimes it is so abundant as to dominate the floor of the woodland, and its rosettes of large wrinkled leaves remain green throughout the summer.

An interesting woodland plant allied to the primrose is the oxlip (*Primula elatior*), which bears a cluster of smaller primrose-like flowers at the end of a tall stalk instead of single flowers as in the primrose. True oxlips are confined in England to two areas on the chalky boulder-clay of north-west Essex, west Suffolk, and south Cambridgeshire, with a few outlying stations to the north. Within these areas every old ash-oak-hazel wood is full of oxlips, and there are a few stations in wet peaty meadows. No primroses exist in these woods except on the edges of the oxlip areas. In such marginal woods where the two species are in contact there is a belt of hybrids between them and there is some evidence that the oxlips are being "pushed back" by the primroses. Oxlips require more lime and water in the soil than primroses. Hybrids between the primrose and the cowslip are often called "oxlips" and bear their flowers in clusters like those of the true oxlip, but they are quite distinct from true oxlips in leaf and flower characters and are found all over the country where their parents grow in proximity, the cowslips in a meadow and the primroses in an adjoining wood.

The common wood violet (*Viola riviniana*) is another very abundant and beautiful woodland species, with

reddish-blue scentless flowers appearing in April. It is perhaps most abundant on the lighter soils and continues to flower, though not so freely, throughout the summer. A closely allied species (*Viola silvestris*) with narrower flowers of a more slaty blue, appearing rather earlier, is found especially on soils rich in lime.

Dog's mercury (*Mercurialis perennis*) and sanicle (*Sanicula europea*) are two other species common on these fertile woodland soils. Mercury begins to grow before winter is over, and its leafy shoots may be found in the south of England pushing up from the underground rhizomes during mild weather in February, with the small green unisexual flowers beginning to open. Its main flowering season is March and April, but, unlike bluebell, wood anemone, and lesser celandine, its erect leafy shoots continue to flourish throughout the summer. Wood sanicle is another common gregarious woodland plant, with rounded and lobed shining leaves and clusters of rather inconspicuous white flowers, growing on similar soils. Like mercury, it keeps its leaves during summer after flowering is over. Both mercury and sanicle, though often found in oakwoods, are specially characteristic of beechwood on shallow chalk soils, where they frequently dominate the field layer.

Other common oakwood species which may be locally dominant in small patches are wild strawberry (*Fragaria vesca*), enchanter's nightshade (*Circaea lutetiana*), and ground ivy (*Nepeta hederacea*). Two beautiful but rather uncommon oakwood plants are the wood forget-me-not (*Myosotis silvatica*), which is most abundant in some of the east Leicestershire woods, with flowers much larger than those of the common field forget-me-not (*M. arvensis*) though smaller than those of the water forget-me-not; and the scrambling wood vetch (*Vicia silvatica*) with cream-coloured and lilac flowers. Besides these, of course, there are a great number of species, which are not gregarious and many of which flower during the summer, belonging to the "central" types of oakwood (medium to damp). To mention only a few of the commoner, we have creeping bugle (*Ajuga reptans*), burdock (*Arctium minus*), three-veined sandwort (*Arenaria trinervia*), wood sedge (*Carex*

silvatica), common willowherb (*Epilobium montanum*), herb-robert (*Geranium robertianum*), archangel or yellow dead-nettle (*Galeobdolon luteum*), woodsorrel (*Oxalis acetosella*), betony (*Stachys officinalis* or *betonica*), stitchwort (*Stellaria holostea*), the speedwells (*Veronica chamaedrys*, *montana*, and *officinalis*); and the grasses *Brachypodium silvaticum*, the tall *Bromus ramosus*, and *Poa nemoralis*, which have no commonly used English names.

On distinctly calcareous but deep soils, such as the chalky boulder-clay of the eastern counties, ash, as has been said (p. 72), is very abundant in the oakwoods—(ash-) oak-hazel woods—but is usually coppiced along with the hazel and other shrubs, so that the oaks are alone dominant in the tree layer. These other shrubs are more numerous both in species and individuals than in oak-woods on non-calcareous soil. They may be called "calcicolous" shrubs, since they are much less frequent and are often absent altogether from non-calcareous oakwoods. They include dogwood (*Cornus sanguinea*), spindle (*Euonymus europaeus*), privet (*Ligustrum vulgare*), buckthorn (*Rhamnus catharticus*), and wayfaring tree (*Viburnum lantana*). The same set of shrubs occurs in ashwoods on limestone soil and in chalk scrub (see pp. 111, 118).

Most of the species and societies of the field layer of these ash-oak-hazel woods on calcareous soil are the same as those of the oakwoods on clays and loams containing little lime, e.g. primrose, anemone, dog's mercury, sanicle, wild strawberry, wood violet, enchanter's nightshade, etc. Dog's mercury is often particularly conspicuous, forming well-marked societies. There are in addition, just as with the shrubs, several species which occur here much more commonly than on non-calcareous soils: nettle-leaved bell-flower (*Campanula trachelium*), calamint (*Clinopodium vulgare*), hairy St. Johnswort (*Hypericum hirsutum*), herb paris (*Paris quadrifolia*), columbine (*Aquilegia vulgaris*), hairy violet (*Viola hirta*), and the early flowering wood violet (*Viola silvestris*). Other more local species of which the same may be said are wood vetch (*Vicia silvatica*), meadow saffron (*Colchicum autumnale*), with leaves appearing in the spring and dying off long before the flowers appear in September, and stinking iris (*Iris*

foetidissima) with large bright red seeds and leaves with a strong garlic-like smell when crushed in the hand—the last two mainly in the west and south-west of England. Most of these, like the calcicolous shrubs, may be found in any tract of calcareous woodland, whether it is dominated by oak or not, e.g. in the pure ashwoods on shallow-soiled limestones. The dominance of oak has nothing to do with their occurrence or absence.

Besides the soil differences, the amount of light reaching the field layer has a primary effect on the species that can flourish in it. The woodland plants proper are those which can tolerate, and in some cases require, relatively good shade; but there are few that are not stimulated to greater luxuriance and especially to free flowering by an increase of light. That is why such characteristically woodland species as wood anemone and primrose flower much more copiously after a wood has been coppiced; and there are many species which can only just "hang on" in deep shade, producing a few weak shoots, but on free access of light immediately burst into vigorous growth and produce abundant flowers. Several of these, though often found in woods, flourish better in all respects when growing in full illumination. Rosebay willowherb (*Epilobium angustifolium*) and foxglove (*Digitalis purpurea*) are two widely distributed species which appear most abundantly and flower most profusely in recently burned or cleared areas of woodland as well as on open commons, especially on light soil. The spikes of bright rose-coloured flowers of the rosebay do not appear in the shade of woods, but the plant maintains itself vegetatively for a long time, spreading by underground rhizomes. It has very small seeds, each with a plume of silky hairs, so that it is widely dispersed by wind and freely colonises vacant building plots in towns, since great quantities of seeds are carried long distances by the wind. It was one of the most conspicuous colonists of the bombed sites in London. Rosebay has a very wide distribution in the northern hemisphere and is one of the plants known as "fireweeds" in North America because it commonly appears in great quantity after a forest fire. Foxglove, which also prefers light (and non-calcareous) soils, is a west European plant and can flower

in the shade of woods, but, like the rosebay, makes the greatest show of flower in open places.

In recently cleared coppice the field layer may be dominated by plants which do not flourish, though they survive, in shade; and of these red campion (*Melandrium dioicum*) and yellow archangel (*Galeobdolon luteum*) are two conspicuous examples, both with very showy flowers, appearing in late spring.

Oakwoods on constantly wet soils are poor in the species hitherto mentioned, many of the ordinary oakwood plants being unable to grow in waterlogged ground. In the tree layer there may be abundance of ash or alder, and such woods grade into alderwood. In the field layer the creeping buttercup (*Ranunculus repens*) and the common stinging nettle (*Urtica diorica*), both common and troublesome weeds of heavy garden soil, may form societies; and in some wet woods meadow-sweet (*Filipendula ulmaria*), much commoner in wet meadows and by stream-sides, may be dominant in the field layer of coppiced woods. Other common species of wet oakwoods are the coarse tufted grass (*Deschampsia caespitosa*) and ragged robin (*Lychnis flos-cuculi*) (both also commoner in wet meadows), moneywort or creeping jenny (*Lysimachia nummularia*) with its circular golden flowers, various rushes (*Juncus*) and sedges (*Carex*), especially the tall drooping sedge (*Carex pendula*), and the weak-stemmed scrambling "cleavers" (*Galium aparine*) with very brittle stems covered with coarse reflexed hairs, so that the shoots, as well as the fruits, easily break off and stick to the clothes of the passer-by.

Very many British oakwoods consist simply of standard trees with a *grassy field layer*, and almost complete absence of the ordinary woodland plants. This is the result of pasturing in the wood, a practice which destroys the natural woodland field layer and prevents the regeneration of trees by destroying their seedlings and by consolidation of the soil through trampling so that it no longer forms a suitable seed-bed for any woodland plant (see p. 16). The grasses found in such woods are not woodland but meadow grasses, and the most abundant is the common bent (*Agrostis tenuis*), one of the most widespread of our grasses, which dominates immense areas of the poorer pastures (see p. 148).

The ground layer of oakwoods contains a considerable number of species of moss. In the medium and damp woods *Catharinea undulata* and *Thuidium tamariscinum* are perhaps the commonest dominants, with species of *Eurhynchium*, *Hylocomium*, and *Mnium*. On more or less calcareous soils *Porotrichum alopecurum* is characteristic in addition to the ordinary mosses. In the heathy woods on acid soils species of *Dicranum* and *Polytrichum*, with *Dicranella heteromalla* and *Hypnum schreberi*, are characteristic. (These mosses have no English names except the Polytricha, which are sometimes called "hair-mosses" because of the hair-like tips to the leaves).

HEATHY OAKWOODS

The heathy oakwoods stand apart from the other types, coming nearest to, but being quite distinct from, the dry oakwoods on light soils whose field layer is dominated by bracken and wood soft-grass (*Holcus mollis*). They are developed on relatively poor acid soils, often light and sandy, and more or less podsolised, and forming a peaty *mor* on the surface from the partly decayed debris of mosses and heath plants. In the north the only common trees other than oaks are birches and mountain ashes. Shrubs are scarce and sometimes practically absent except for occasional sallows (*Salix atrocinerea* and *S. aurita*) and in southern England the alder buckthorn (*Frangula alnus*). The field layer is often dominated by bilberry (*Vaccinium myrtillus*), which tolerates some shade, with heather (*Calluna*) in open places. Both of these are undershrubs belonging to the heath family. A very characteristic plant of heathy woods is the wavy hair-grass (*Deschampsia flexuosa*) with fine bristle-like leaves and elegant loose inflorescences bearing minute spikelets. Bracken is usually abundant, and tormentil (*Potentilla erecta*) with its small neat yellow flowers shaped like a Maltese cross, and heath bedstraw (*Galium saxatile*) with tiny white flowers, are common in open places. The purple moor-grass (*Molinia caerulea*) is often locally dominant in heathy woods where the water level is close to the surface.

The heathy oakwoods of southern England are dominated by either species of oak or by both together. They are common on deep sands in the Weald and in the London and Hampshire basins; but on these soils the oaks are often accompanied not only by the birches but also by pine and beech, where woods of these trees are present in the neighbourhood (see Chapter VIII, p. 129, and Phots. 81, 82). The heathy oakwoods of the north and west are mostly on sandstones and grits, especially at the higher altitudes, and are all dominated by the sessile oak (Phot. 6).

THE KILLARNEY OAKWOODS

The oakwoods near Killarney in south-western Ireland (Phots. 11-14) have been closely studied and are of great interest, for they are undoubtedly natural woods and, while there has been some felling of trees in the past, they have been very much let alone for many years. They are based on Lower Devonian sandstones and shales, and the soil shows different stages of podsolisation.

The best grown woods, on but slightly podsolised soil, are dominated by sessile oaks with the trees nearly 70 feet high and just far enough apart for the crown of each to be spreading but in contact with neighbouring crowns. Other trees (birch and mountain ash) are sparse or rare, but yews 50 feet high are scattered thinly through the oakwood. Below the canopy is a continuous stratum of holly 20 to 30 feet high (Phots. 13, 14). These two continuous strata of foliage reduce the light reaching the ground to a point at which no well-developed field layer can exist. There are only 8 species in all, and these are represented by an occasional plant rooted round the large boulders of which the substratum of the wood is mainly composed. Of these plants only bilberry, great woodrush (*Luzula maxima*)—a very common plant in woods on the old rocks of the west—woodsorrel, and the fern *Dryopteris aemula* are frequent, but the growth of the two former is very poor and they never produce flowers. On the other hand, the moss and liverwort vegetation is extremely rich and abundant, covering the boulders and the trunks and branches of the oaks with a thick mantle (Phot. 12). No less than 26 mosses

R. J. Lythgoe

PHOT. 11. Derrycunihy wood of durmast oak and holly on an Old Red Sandstone hill near the Upper Lake, Killarney

R. J. Lythgoe

PHOT. 12. In the Upper Woods, Killarney. A dense carpet of mosses covers the boulders and tree trunks. Thick ivy stem climbing tree on the left. Few flowering plants: one foxglove on the right.

Elizabeth Cowles

PHOT. 13. Oaks in close canopy with continuous layer of holly below. Bracken in foreground outside the wood.

Elizabeth Cowles

PHOT. 14. Closer view of holly layer. Ivy climbing the oak trunk.

Face p. 91

and 30 liverworts have been recorded, together with 2 species of filmy fern (*Hymenophyllum tunbridgense* and *H. unilaterale*). The mosses form the great bulk of this ground stratum, *Hylocomium brevirostre*, *H. loreum*, and *Thuidium tamariscinum* being frequently co-dominant on the boulders. The luxuriance of the bryophytic vegetation is of course due to the very damp air of the habitat caused by the wet climate combined with the deep shade of the woods.

In woods where the soil is more deeply podsolised and therefore less fertile, there are many more oaks to the acre, but these do not grow so tall and thick; and there is an increase of other trees (birch and mountain ash). The canopy is discontinuous, and the holly stratum also, so that more light penetrates. Accordingly the field layer is better developed, bilberry grows more luxuriantly and so does bracken, while heather (*Calluna*) becomes dominant in the more open places and a few other species occur.

On thoroughly podsolised soils there is a low mixed wood consisting of oak, mountain ash, birch, and holly, with occasional strawberry tree (*Arbutus*), and in these the oaks, though numerous, are no longer dominant, and no trees reach a height of more than 25 feet. The field layer is now closed and is formed mainly of heather, bilberry, and bracken, with abundance of great woodrush and hard fern (*Blechnum spicant*) and scattered individuals of 10 other species (largely those characteristic of heathy woods).

The series described well illustrates increasing poverty of the tree-growth and approximation to the heathy type of flora with increasing depth of podsolisation.

The strawberry tree (*Arbutus unedo*), with its laurel-like leaves, racemes of pink bell-shaped flowers and succulent, "flat"-tasting and slightly nauseous fruits, is a western Mediterranean species very common as a shrub of the scrub or *mâquis* characteristic of that region. In the British Isles it is now confined to parts of south-west Ireland, where it grows more luxuriantly than in the mâquis, forming a tree which may reach a height of 30 feet. This is because of the cool damp equable climate, which does not check its growth like the Mediterranean summer drought. The winter minimum temperatures are about the same in

both regions, so that *Arbutus* escapes severe frost, which it will not tolerate. The strawberry tree colonises clefts in the rocks and becomes surrounded by heather and then by holly rooted in the accumulating acid humus soil. The oaks presently establish themselves and gradually build up a canopy in which *Arbutus* cannot survive. Its position is thus always *marginal* to the well-developed oakwoods.

Laurel-leaved trees such as holly and arbutus are characteristic of the damp oceanic temperate climates of which the climate of south-western Ireland is a very marked example. This feature of the climate is emphasised by the prevalence and luxuriance about the woods of other evergreen shrubs with laurel-like leaves which are not native in the British Isles, such as Portugal laurel (*Prunus lusitanica*), cherry laurel (*Prunus lauro-cerasus*), and the bay or "true laurel" (*Laurus nobilis*), as well as the common rhododendron (*Rhododendron ponticum*) which multiplies freely from seed in parts of the Killarney woods.

Another feature of the vegetation is the comparative abundance of epiphytes [1] on the oaks at Killarney, not only the thick mantles of mosses and liverworts, but also ferns and flowering plants. The following have been noted: filmy ferns (*Hymenophyllum tunbridgense* and *H. unilaterale*), polypody (*Polypodium vulgare*), herb-robert (*Geranium robertianum*), a saxifrage (*Saxifraga spathularis*), and of woody plants holly (*Ilex aquifolium*) and rhododendron (*Rhododendron ponticum*).

OAKWOOD UNDER EXTREME CONDITIONS

The extreme limit of altitude now reached by oakwood in England is less than 1500 feet, both on Dartmoor in the south-west and in the Cumbrian Lake District. On Dartmoor there are three small woods not far short of this altitude. The best known is Wistman's Wood near Two Bridges, consisting of fragments of the old native oakwoods which once clothed the hillsides of this region and have nearly all been destroyed, largely by tin-miners. Wistman's Wood (1200-1380 feet) clings to the steeply sloping eastern side of the valley of the West Dart (Phot. 15) and consists

[1] Epiphytes are plants growing on, but not parasitic upon, other plants.

R. J. Lythgoe

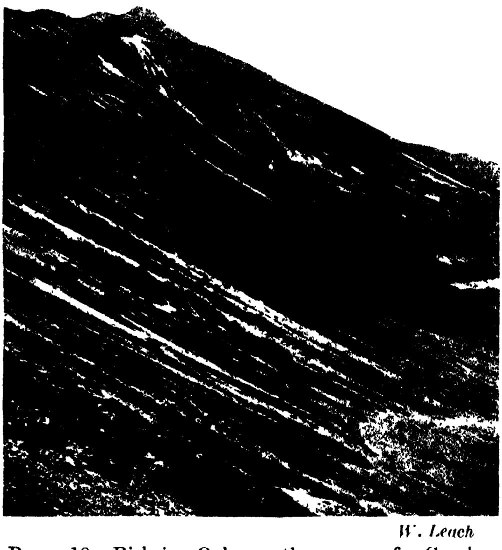
PHOT. 15. Part of Wistman's Wood, 1200 1400 ft. alt., along the steep slope of "clatter," above the West Dart. Open moor beyond, with Littaford Tor on the skyline.

R. J. Lythgoe

PHOT. 16. Great woodrush, woodsorrel, broad buckler fern, ivy, corydalis, between the boulders on the floor of the wood.

R. J. Lythgoe

PHOT. 17. An old contorted oak in Wistman's Wood. A thick mantle of mosses, with polypody fern, bilberry, and mountain ash, growing on the tree.



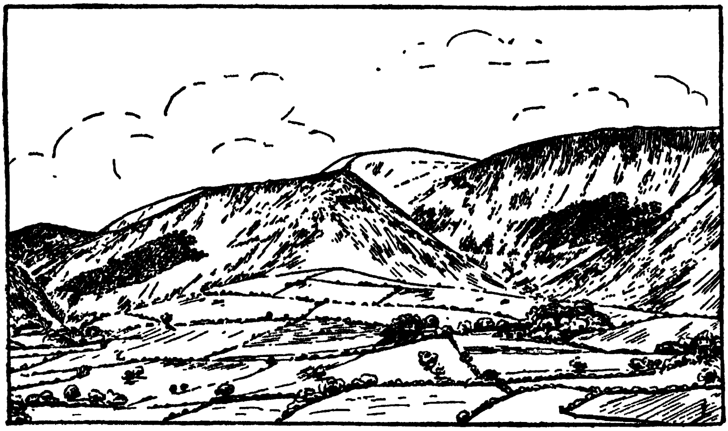
W. Leach

PHOT. 18. Birkrigg Oaks on the screes of a Cumberland mountainside at 1200–1400 feet alt. Compare the situation of Wistman's Wood (Phot. 15).

of dwarf pedunculate oaks rooted between great granite boulders and just managing to exist under extreme conditions of exposure to wind. The roots and often the trunk and main branches of the oaks are wedged in the clefts between the boulders or lie horizontally upon their surfaces, and only in this way can the trees maintain themselves. The average height above ground level attained by the branches is between 14 and 15 feet, while the average girth of the trunks is over 4 feet. The tallest tree in the wood is only 26½ feet high, with the relatively enormous girth of 8½ feet. One isolated tree is only 10 feet high, but its crown has a spread of 25 feet. On the eastern edge of the wood, however, which is relatively protected from wind, seedlings can establish themselves and grow up into saplings, some of which are pyramidal in shape, like any young oak growing in normal conditions, but are of very slow growth. One of these is 18 feet high and 16 inches in girth near the base, another 25 feet and 19 inches round the base. All the trees are therefore very old for their height: the oldest have been estimated at 500 years.

Besides this extreme dwarfing and great thickness of the trunks, a feature which at once catches the eye is the thick mantle of mosses and liverworts that covers the branches (Phot. 17), among which grow no less than 7 species of ferns and flowering plants—a striking proportion of epiphytes in the total flora of the wood, which numbers less than 30 species of higher plants. The humus which accumulates on the thick horizontal branches is very much the same as that on the boulders, which are also covered with a mantle of mosses, so that the two habitats are closely similar. (Cf. the Killarney woods.)

There are very few trees or shrubs besides the oaks—a few mountain ashes, which occasionally grow in the crotches of the oaks, one or two hollies, and a few grey sallows: ivy and honeysuckle are, however, frequent. The field layer contains 28 species, the only abundant plants being bilberry on the rocks and the great woodrush in the deeper shade. More than a quarter of the species of vascular plants are ferns, which are conspicuous in the wood. Photograph 16 shows a sample of the field layer, including great woodrush, woodsorrel, ivy, broad buckler



W. Leach.

FIG. 1. Birkrigg and Keskadale Oaks at 1000-1500 feet on the slopes of Causey Pike and Ard Crags in Cumberland. Birkrigg Oaks are seen to the right (cf. Phot. 18) and Keskadale Oaks to the left.

fern, and the pretty white-flowered scrambling corydalis (*C. claviculata*). The similarity of this vegetation, particularly the luxuriant abundance of mosses and epiphytes, to that of the Killarney oakwoods is clear, both being developed in a very wet climate.

Birkrigg and Keskadale Oaks on the screes of the southern slopes of Causey Pike and Ard Crags in Cumberland, at about the same altitude, are composed of sessile oaks. Birkrigg Oaks are shown on the right in Fig. 1, and in the distance in Photograph 18. The soil is shallow and stony but not composed of boulders. The Birkrigg trees have multiple stems as if coppiced, but this is really due to previous destruction by burning or disease and fresh suckering from the stools. The height of Birkrigg Oaks averages only 12 feet and the girth of the stems 36 inches, so that the low ratio of height to girth and height to age is seen again here, though not to such an extreme degree as on Dartmoor. Mountain ash is occasional in both Birkrigg and Keskadale Oaks, and there are no other accompanying trees. Burning of parts of the wood is not uncommon, and oak seedlings are rare. It is not clear that the woods regenerate as Wistman's Wood does. The field layer contains 18 species of flowering plants and ferns, nearly all of the heathy type, and 12 of

these are common to the two Cumbrian woods and Wistman's Wood. Bilberry, bracken, and wavy hair-grass are the three most abundant plants, and heather occurs inside the woods, while it is absent from Wistman's Wood. There are 49 species of mosses and liverworts, and these are locally dominant on the more shady parts of the wood floor. Some are epiphytic on the oak trunks, but they do not cover the trees so thickly as in Wistman's Wood, probably because much more light penetrates the wood and the air is not so constantly damp.

VARIETIES OF OAKWOOD

The range of oakwoods described in the preceding pages—the heathy oakwoods last mentioned, those on light dry soils with wood soft-grass, bluebell, bramble, bracken, etc., and the medium and damp types with better soil and a rich and varied flora—may be dominated by either species of oak, and in the heathy woods of the south by both species together, but in the pedunculate oakwoods the two last-named types are much the commoner. This is because pedunculate oakwoods occur mostly on more or less fertile clays and loams which the characteristic field-layer plants—mercury, sanicle, anemone, primrose, etc.—also naturally inhabit. The sessile oakwoods of the north and west are mostly either bracken and soft-grass woods or heathy woods, developed on coarse grits and sandstones and other hard rocks, poor in nutritive minerals and yielding light soils; while the better types of these sessile oakwoods are confined to the shales yielding a heavier damp soil which is much less extensive in northern and western Britain. The two oaks have no specific differential effect on the shrub and field layers—either oak may dominate a wood in which any type of shrub and field layer is present. Soil type, and perhaps to some extent climate, determine the occurrence of one oak or the other, and soil type, together of course with light supply, also determines the type of shrub and field layer. Owing to the different geology and to some extent the different climate, the *prevalent* soil type of the north and west of Britain is very different from that of the English midlands, south and east, and hence the *prevalence* of sessile oakwood and particular kinds of field

layer in the one region, and of pedunculate oakwood and other kinds of field layer in the other.

The oakwood flora includes the overwhelming majority of British woodland plants. Very few species, though there are a few, occur only in other kinds of woodland—the beechwoods, the ashwoods, or the pine and birch woods of the north. The alderwoods on wet soil, though they show transitions to wet oakwoods, have a more distinctive flora and vegetation because of the widely different conditions imposed on plants growing in permanently, or almost permanently, waterlogged soil.

SUCCESSION

The natural development of oakwood on new ground, i.e. the succession of plant communities leading up to oakwood, varies, of course, according to the soil on which it takes place. On the rocks round the Killarney lakes we saw that the sessile oakwood was preceded by arbutus and communities of heather and then of holly, among which the oak seedlings establish themselves. In closely cultivated country the natural development of oakwood is so rarely let alone that the available information is very scanty, but on abandoned clay pastures there is initial colonisation by dog-rose, gorse, and hawthorn, the loose scrub formed by these shrubs being colonised by oaks, whose saplings eventually shade out and kill the pioneer shrubs. The characteristic oakwood shrubs invade the wood together with the oaks, but only later, when the dense woody canopy has "opened out," is any considerable field layer developed. Very often the development of oakwood is checked by cutting of the young saplings and the scrub stage is prolonged. A great number of herbaceous species are then met with in the scrub, including those which have survived from the original pasture, a large number of marginal or "semi-shade" species, and true woodland shade plants (see pp. 184-5). The same sort of thing happens when arable land is abandoned or heathland left alone. The scrub which develops then has a field layer of arable "weeds," or of heath plants, with marginal species, and also the forerunners of the true woodland shade flora.

CHAPTER VII

THE ENGLISH BEECHWOODS

Chalk Scrub and Yew Wood

WHILE the oak-hazel coppices provide the finest shows of spring flowers, there is nothing more beautiful and satisfying than a beechwood at all times of the year. In May the tender translucent green of the young leaves, in high summer the cool shade beneath the heavy deep green canopy supported by the smooth grey pillar-like boles; the glorious golden bronze of the autumn foliage, and the no less gorgeous purple of the carpet of wet fallen leaves lighted by the low sun of a winter afternoon following rain, with tracery of bare slender twigs against the sky above—there is nothing in English woodland scenery that excels the splendid seasonal pageant of the beechwood. The very "emptiness" of the wood caused by the dearth of shrubs (Phots. 19, 28), combined with the striking grace and beauty of the tree trunks, gives a unique simplicity and dignity to the scene. For their loveliness alone we ought to preserve our few beechwoods with jealous care.

It is only recently that we have been quite certain of the genuine "nativity" of beech (*Fagus silvatica*) in England. Previously there were a few records of prehistoric beech charcoal, but some doubt had been cast on their reliability, and Caesar's remark that the Gallic trees were found in Britain except beech and fir strengthened the doubt, since Caesar certainly traversed country where beechwood exists to-day. But charcoal from a pre-Roman Iron Age site in South Wales has now been definitely determined as beech charcoal, and there are also several records of beech pollen from Sub-Atlantic and even Bronze Age peats. East Anglian sites show the greatest quantity, though the pollen occurs as far west as Devonshire and South Wales and as far north as Durham. In south-eastern England, where beech is well established now but where Caesar did not see it, there are, unfortunately, few

peat deposits from which the history of the tree in that region might have been reconstructed. There seems no doubt, however, that beech was widely distributed through England and Wales between 2000 and 3000 years ago, though whether it formed independent woods of any extent remains uncertain: in East Anglia at least, however, it is highly probable that it did. In Ireland it seems never to have been present as a native tree.

As a dominant aggressive tree, forming extensive woods and suppressing rival trees, beech is now confined to southern and mainly to south-eastern England. In other parts of the country, apart from beech plantations, more or less isolated beeches are met with, many no doubt planted, but others quite possibly the descendants of native trees.

The principal existing regions of beechwood are: (1) the chalk round the Weald in Kent, Surrey, Hampshire, and Sussex; (2) the Chiltern Hills and the adjacent chalk of the Thames valley; and (3) the central stretch of the Cotswold Hills. A large proportion of these woods are on the shallow chalk or oolitic limestone soils of the escarpments and valley-sides, though some are on the deeper and frequently non-calcareous loams covering the plateaux. There are also small outlying areas of beech, which is probably natural, in the Wye valley and in South Wales, on Mountain Limestone and on Old Red Sandstone. Comparatively small areas of beechwood also occur on the sands of the south-east—in the Weald and on the edge of the London basin and on similar soils in the Hampshire basin (New Forest). Outside these areas beech is only found in small plantations and as isolated trees, though some of these latter, as has been said, may well be relics of a former much more widespread distribution of beechwood.

Because of the occurrence of the great bulk of existing English beechwood on chalk and limestone soil it has often been said that beech has a "preference" for calcareous soil, but this is a mistaken notion. Beech tolerates and forms quite good trees on the shallow soil of the chalk escarpment, while oak does not, but beech can grow very well on non-calcareous soils and even on strongly acid sands. Like most other trees, it does best of all on deep fresh fertile loam irrespective of high lime content. The only soil which

beech will not tolerate is waterlogged soil, and for this reason it is very rarely found on heavy clays which are often waterlogged in winter. Here it cannot compete with oak, just as oak cannot compete with beech on the dry shallow soils of the chalk escarpment. Owing to its success on a variety of soils, three types of beechwood may be distinguished: first, those on shallow calcareous soils (rendzinas); secondly, on deep loams (brown earths); thirdly, on acid sands, more or less podsolised.[1] The accompanying trees, shrubs, and woodland herbs of these three types show distinct and sometimes wide differences.

BEECHWOOD ON SHALLOW CHALK SOILS

Beechwoods of the first type grow on the steep escarpments of the Chiltern Hills and of the chalk downs fringing the Weald, as well as on the steeper chalk valley-sides, and also on the escarpments, slopes, and plateaux of the Cotswold oolite. In east Hampshire and in west Sussex these beechwoods on steep hillsides are known as "beech hangers." The trees do not grow very tall—the soil is too shallow—seldom exceeding about 70 feet. The wood is usually very pure, consisting almost entirely of beech: a few ashes are often present in the canopy, but always as thin stems of poor growth, "drawn up" to the light by the deep shade of the surrounding beeches. The whitebeam (*Sorbus aria*) often holds its own with beech in the canopy. In a naturally developing wood both these trees are survivors from an earlier stage of succession, before the beech established dominance. Gean or wild cherry (*Prunus avium*) is frequent in the Chiltern escarpment woods, and its masses of white flower make a conspicuously beautiful feature in early May.

Of smaller trees spreading their foliage below the shade of the beech canopy the two evergreens, holly (*Ilex aquifolium*) and yew (*Taxus baccata*), are characteristic species, though they do not occur in all escarpment beechwoods. These evergreens, of course, gain an advantage by being able to vegetate in the spring before the foliage of the beech canopy is fully expanded. Locally either yew or

[1] For explanation of these terms see pp. 37-40.

holly may form a dense layer well below the crowns of the beeches (Phot. 20). Ivy (*Hedera helix*) is just as common as in oakwoods (p. 79), either climbing the trees or creeping on the ground, where it may be locally dominant in the field layer.

A fourth evergreen sometimes found in calcicolous beechwoods is box (*Buxus sempervirens*) with small oval leaves, notched at the tip. When growing freely in the open, box is a tall shrub or small tree 15 to 20 feet high. It is abundant on the limestone hills of central and southern France, but it does not appear to be indigenous in the north, and as a wild plant it is rare in England, where, however, it is probably native on the southern chalk and oolite, occurring here and there as a low shrub under the shade of beech. Box is abundant in association with yew and beech on Box Hill near Dorking in Surrey, where the woodland has all the appearance of a fragment of the old native forest of the chalk escarpment. It is also abundant in the open on the escarpment of the Chilterns near Little Kimble in Buckinghamshire. At Boxwell on the Inferior Oolite of the southern Cotswolds in Gloucestershire there is a boxwood at least seven centuries old which is regularly coppiced on a 30-year rotation. Even if it has a native nucleus this coppice has certainly been extended by planting, since part of it has the shrubs in regular rows. Boxwood is a hard, heavy, close-grained wood, much valued from ancient times, and used for turnery in the making of small ornamental wooden objects and for wood engraving. It has been much planted for the sake of the wood and is a traditional garden shrub for hedges and edgings, since it tolerates frequent trimming. For these reasons it is impossible to be quite certain of its status as a native shrub in most of its English localities.

Deciduous shrubs are scarce and often quite absent in the escarpment beechwoods. Elder (*Sambucus nigra*), field maple (*Acer campestre*), hazel (*Corylus avellana*), and spindle (*Euonymus europaeus*) are the commonest. The other calcicolous shrubs (p. 86) rarely occur inside beechwood except in openings where they can get more light. Besides the poor light, another important cause of the paucity of shrubs (and often of the field layer too) is the intense

C. J. P. Cave

PHOT. 19. Beechwood on chalk slope in winter. Oakham Bottom, Ditcham Park near Petersfield, Hants.

R. J. Lythgoe

PHOT. 20. Dense layer of yew growing below beech on chalk escarpment. Duncton Down near Petworth, Sussex. April.

A. G. T.

PHOT. 21. Beechwood on chalk escarpment with field layer of dog's mercury. The Miscombe, Ditcham Park, Hants.

R. J. Lythgoe

PHOT. 22. Top of beechwood on chalk escarpment with field layer of sanicle. The floor of the plateau beyond (also bearing beechwood) is here bare. Pulpit Hill, Chiltern escarpment, Bucks.

competition of the beech roots, which fill the shallow soil with their fine fibrous branches and drain it of water, so that after a period of dry summer weather the rest of the vegetation suffers seriously from drought.

In a young beechwood in which the saplings are closely set the field layer is absent except for a few weak scattered plants, but as the trees grow up and the canopy opens out the floor of a calcicolous beechwood is usually colonised by quite a rich flora including several characteristic species, though most of the plants are the same as those of oakwoods on fertile soil. Two species (both common in damp oakwood) are generally dominant—dog's mercury (*Mercurialis perennis*) (Phot. 21) on the deeper soils and gentler slopes, and sanicle (*Sanicula europaea*) (Phot. 22) on the shallower soils and steeper slopes. Where mercury grows luxuriantly its closely set leafy shoots, as much as a foot high, tend to exclude other species, especially those of low growth. In the "sanicle woods" there is a greater variety of species, including "rosette plants" whose foliage is confined to a rosette of leaves close to the ground, and there are many more mosses, which are largely excluded in "mercury woods."

Common spring-flowering plants abundant in calcicolous beechwoods as well as in oakwoods are wood anemone (*Anemone nemorosa*), cuckoo-pint or lords-and-ladies (*Arum maculatum*), wild strawberry (*Fragaria vesca*), and archangel or yellow dead-nettle (*Galeobdolon luteum*). These all produce their leaves early and flower at some time from March to May. Two other plants common in beechwoods are wood spurge (*Euphorbia amygdaloides*), which shoots in April and flowers in May, and enchanter's nightshade (*Circaea lutetiana*), which forms its leaf-rosettes in April and May, but produces its tiny pinkish-white flowers, loosely arranged on a tall inflorescence, in the summer. All the species mentioned (none of which is peculiar to beechwood) are able to carry on their vegetative activity in plenty of light before the dense canopy of beech foliage closes in. Other common woodland species frequently occurring in beechwoods, but again not at all peculiar to them, flower in late spring or summer, such as creeping bugle (*Ajuga reptans*) with its spikes of deep blue flowers, the germander

speedwell (*Veronica chamaedrys*) with bright sky-blue corollas, quickly shed, the paler-flowered *Veronica montana*, herb-robert (*Geranium robertianum*), wood sedge (*Carex silvatica*), and the grasses *Brachypodium silvaticum*, *Bromus ramosus*, and *Poa nemoralis*.

Much less common plants which are distinctly characteristic of calcicolous beechwoods, though not strictly confined to them, are green hellebore (*Helleborus viridis*), columbine (*Aquilegia vulgaris*), Solomon's seal (*Polygonatum multiflorum*), and an evergreen dwarf shrub, the spurge laurel (*Daphne laureola*), which produces small green flowers in early spring. Very characteristic of beechwoods, though again not confined to them, are sweet woodruff (*Asperula odorata*)—very fragrant if crushed in the hand, and producing small pure-white 4-pointed flowers—the early-flowering wood violet (*Viola silvestris*) with its rather narrow slaty-blue flowers, and the large-leaved hairy violet (*Viola hirta*), wall lettuce (*Lactuca muralis*), the leaves with sharply pointed lobes, and melic grass (*Melica uniflora*).

Most characteristic of all, however, are certain orchids—common helleborine (*Epipactis latifolia*), white helleborine (*Cephalanthera grandiflora*), which occurs in almost every old escarpment beechwood and is apparently confined to them, and the rare narrow-leaved helleborine (*Cephalanthera longifolia* or *ensifolia*). The yellowish-brown bird's-nest orchid (*Neottia nidus-avis*)—always looking rather as if it were a dead plant—and the pale cream-coloured "bird's nest" (*Monotropa hypopitys*), which is allied to the heath family, are pure saprophytes [1] that never produce chlorophyll (the green pigment of leaves) and are able to grow in the heaviest shade. All these flourish only in deep humus and are highly characteristic of beechwoods.

The ground or moss layer of the escarpment beechwood is never continuous and is often restricted to the lower parts of the tree trunks, the upper surfaces of the main roots which diverge horizontally from the bases of the trunks, and the ground immediately around. Mosses cannot establish themselves in the thick leaf litter which covers most

[1] Saprophytes are plants which do not make their own food, as green plants do, but, with the aid of fungi, get it directly from the organic constituents of humus.

of the floor of the wood. *Hypnum cupressiforme* on the bases of the beech trees and *Hypnum molluscum* on the soil are the two most widespread and abundant species, but there are a great many others, especially in the "sanicle woods" where there is more room for them between the flowering plants and often more mineral soil close to the surface.

The soil of calcicolous beechwood is very characteristic. The surface is covered with a thick layer of beech-leaf litter, 2 to 4 inches deep, except where the wind sweeps it away leaving the mineral soil bare, or where the leaves collect in hollows and the litter is much deeper. This passes down into a thick layer of dark brown or black humus which is distinctly alkaline and in which minute particles of chalk may often be seen. Below the humus come several inches of pale brown highly calcareous mineral soil in which the chalk particles become larger and more numerous as the weathered surface of the underlying chalk rock is approached at 12 to 16 inches from the surface. The humus layer and the underlying mineral soil are very thoroughly penetrated by the fibrous feeding roots of the beeches. Stout anchoring roots strike downwards into the fissures of the chalk.

In young woods where the shade is very deep and the soil very completely permeated by fibrous beech roots, the ground is often nearly or entirely destitute of vegetation, the continuous brown leaf litter being unbroken, or interrupted only by a single plant here and there—sometimes the "bird's nest" (*Monotropa*) or the bird's-nest orchid (*Neottia*). The white helleborine (*Cephalanthera*) can also grow in very deep shade. Where the slope is very steep and the litter cannot lie, the floor of the wood is bare white chalk soil which becomes extremely dry in summer and bears nothing but an occasional moss. On the exposed edge of a wood and wherever strong winds have access the same conditions exist.

The white or pale brown sheaths of "mycorrhiza," formed by the delicate "hyphae" of the fungi associated with tree roots, are extremely abundant on young beech roots, especially in the humus layer, which is invaded in late winter and very early spring by the growing tips of

the young roots, which are soon afterwards infected by mycorrhizal fungi. These fungi produce large mushroom-like fructifications later in the year, belonging as they do to the class of fungi (*Basidiomycetes*) which includes the common mushroom and the "toadstools." In early summer the shallower soils tend to dry up and arrest the growth of the young roots and their mycorrhiza. Besides the fungi associated with the living beech roots, many other kinds of the larger fungi live in the humus of the escarpment woods. Of these the most characteristic are *Collybia radicata*, *Marasmius peronatus*, and *Mycena pura*, which are abundant, and *Cortinarius calochrous*, *Hygrophilus eburneus*, and *Mycena pelianthina*, which are less common. The two species of *Mycena* are apparently dependent on free calcium carbonate in the soil, and the *Cortinarius* seems to be confined to the escarpment woods.

BEECHWOOD ON DEEP LOAMS

Beechwoods of the second type are found on the deep loams overlying the chalk plateaux on the South Downs of west Sussex and Hampshire and on the Chiltern Hills in Buckinghamshire and Oxfordshire. These loams belong in general to the "brown earth" type of soil (see p. 88). Some of the shallower plateau soils of the South Downs are not much deeper than the deepest escarpment soils, and contain a fair amount of calcium carbonate, while the Chiltern plateau soils are quite destitute of it and are in fact markedly acid, but they both agree in being rich in nutritive mineral elements; and this, with the fact that the soil is deep, and does not dry out readily, makes them very fertile. Some of these plateau soils bear the finest beechwoods we have (Phot. 28), the mature trees being well over 100 feet in height and with an average girth of more than 5 feet. It is in these woods on the Chiltern plateau that the old industry of chair-making is still carried on (Phot. 24). Oak (*Quercus robur*) is often present and reaches a height equal to that of the beech. The presence and luxuriance of oak in these woods is in sharp contrast to conditions in the shallow-soiled escarpment woods from which oak is practically absent. Ash is pre-

BEECHWOOD ON DEEP LOAM

R. J. Lythgoe

PHOT. 23. Plateau beechwood on deep loam with finely grown beech of more than 100 ft. layer of bramble, etc. Hailey Wood, Oxon.

The Times

PHOT. 24. Chair bodgers in the beechwoods of the Chiltern plateau. Field layer of bramble.

R. J. Lythgoe

PHOT. 25. Stinkhorn fungus in beechwood humus on the Chiltern plateau. Bramble and woodsorrel. Kingston Wood, Oxon.

sent in the woods on the less acid soils and also reaches the height of the canopy, as does gean (*Prunus avium*). Whitebeam is sometimes present, and hornbeam (*Carpinus betulus*) in the northern Chiltern woods.[1] In some of the woods on the South Downs, sycamore (*Acer pseudoplatanus*) is present and competes with beech for dominance, recalling the beech-maple (the American beech, *Fagus grandifolia* and the sugar maple, *Acer saccharum*) forest of the eastern United States, though in England sycamore is not a native tree. Of trees of lower stature, yew is much less common than in the escarpment woods and on the Chiltern plateau is almost absent. Holly occurs, and on the South Downs occasionally forms a lower tree layer. But on the whole the plateau woods are even emptier of low trees and shrubs than the escarpment woods.

A characteristic feature of the plateau woods is the presence of an upper field layer of bramble which may form an almost continuous cover from 1 to 2 feet high. Where the shade of the canopy is too dense to permit such dominance of bramble, the woodsorrel (*Oxalis acetosella*), whose very delicate clover-like leaves are well adapted to deep shade, may be dominant on the ground. Photograph 25 shows the bramble and woodsorrel and a "stinkhorn" fungus in the deep beech leaf litter. Of other species there are a great number, including several of those characteristic of escarpment woods, such as mercury, sanicle, wild strawberry, sweet woodruff, archangel, and, on the Chiltern plateau, also species characteristic of acid soils, such as bracken and foxglove, while bluebell (*Scilla non-scripta*) may be locally dominant, and in the more open places the common bent (*Agrostis tenuis*) and the wood soft-grass (*Holcus mollis*).

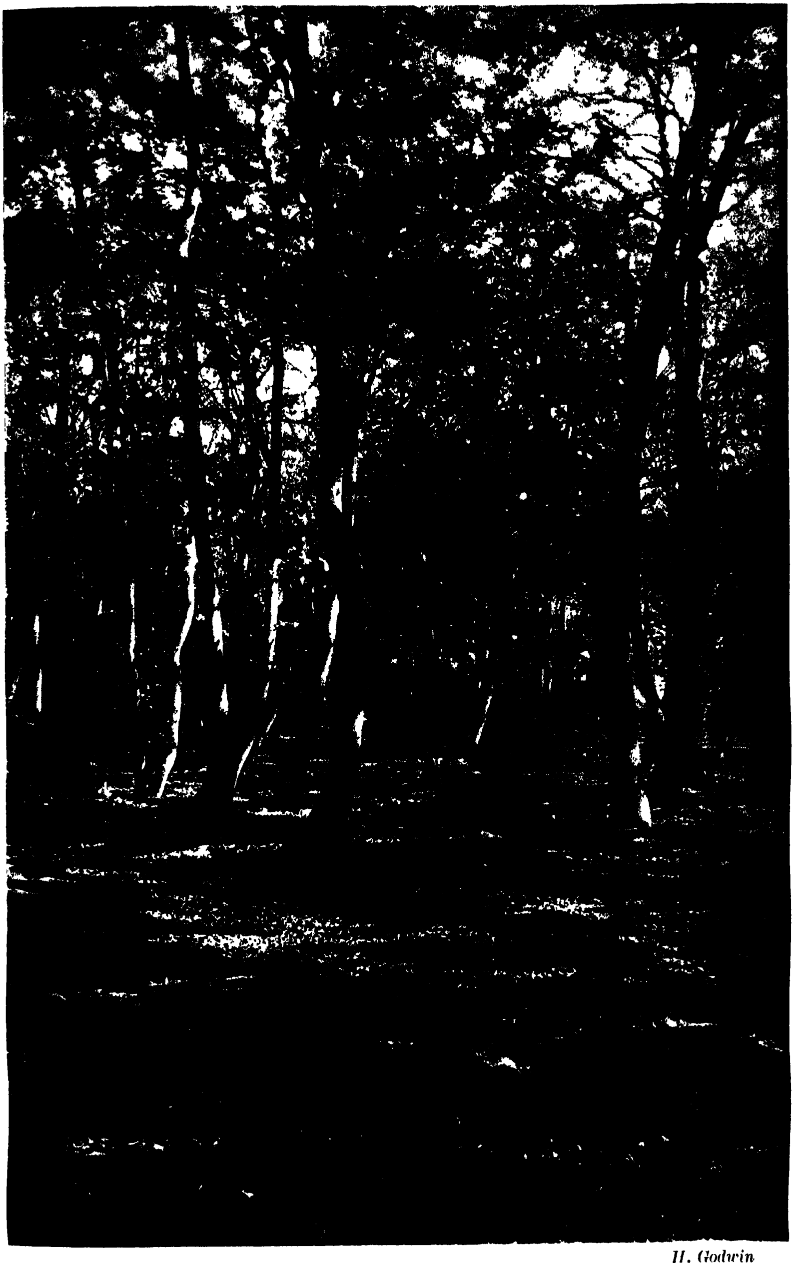
The tall handsome wood-grasses *Bromus ramosus*, *Elymus europaeus*, *Festuca gigantea*, and *Milium effusum*, whose leaves and general appearance have a strong family resemblance, are rather common in the Chiltern plateau woods; and the coarse harsh-leaved tufts of *Deschampsia caespitosa* are quite frequent on the close-grained soils, especially where water stands in winter, but this grass does not flower in deep shade.

[1] Near the western limit of the south-eastern hornbeam area (see p. 73).

There are far fewer mosses and liverworts than in the escarpment woods, partly because of the prevalence of the bramble cover and partly because of the more continuous leaf litter. The mycorrhiza of the beech roots, which is equally abundant in the humus of the plateau woods as in that of the escarpment woods, continues its growth with that of the young roots throughout the summer except during particularly severe droughts. Of the larger fungi, *Collybia butyracea* and *C. platyphylla, Russula atropurpurea* and *R. cyanoxantha* are frequent, and *Laccaria laccata* and its variety *amethystina, Mycena galopus* and *M. sanguinolenta* are often abundant, the two last-named apparently requiring the moist still air between the bramble shoots. All eight kinds are characteristic of the plateau beechwoods.

BEECHWOOD ON PODSOLS

While the fertile clays and loams of the chalk plateaux clearly belong to the "brown earth" type of soil, there are more silty soils on the Chiltern plateau which show various degrees of podsolisation, and on these more intensely acid soils the third type of beechwood is developed. The beeches are not nearly so well grown, not more than 60 feet in height, of much smaller girth, often crooked, and with dark, rougher bark, and there are more trees in a given space. (Photograph 26, actually taken from a beechwood of this type on gravel at Burnham Beeches, shows the crowded beeches with this crooked habit.) The oaks accompanying the beeches are of equal height or somewhat taller, so that they project above the beech canopy. Ash, whitebeam, and hornbeam are absent, and gean finds no place in the canopy. The total number of woody species is small, not half that occurring in the second type of beechwood. *Salix aurita* is the only shrub found here and not in the previous type. Holly is, however, common, and often takes the form of a low procumbent bush. The field layer is absent over great stretches of these woods, and the more "exacting" plants, i.e. those which only grow on the more fertile soils, are absent. In their place we have the characteristic plants of highly acid soils, such as the wavy hair-grass (*Deschampsia flexuosa*) with its bristle-like leaves,



H. Godwin

PHOT. 26. Beechwood on gravel with badly grown crooked trunks. Ground covered with leaf litter and large cushions of the moss *Leucobryum*. Burnham Beeches.

The Times

PHOT. 27. Old pollard beeches on gravel at Burnham Beeches. Mosses and leaf litter on the ground.

A. S. Watt

PHOT. 28. Mature beechwood on drained heath in Aberdeenshire. The trees have sown themselves from plantations. Mountain ash on the left. Field layer of bilberry.

the "pill sedge" (*Carex pilulifera*), the upright St. Johnswort (*Hypericum pulchrum*), and in more open places the common ling (*Calluna vulgaris*). The mosses also are those characteristic of acid soils, especially *Hypnum schreberi* and *Leucobryum glaucum* (Phot. 26), with increased abundance of *Polytrichum formosum*. The plenitude of these "hair-mosses" (*Polytrichum*) is always an index of increased acidity. Of liverworts the leafy *Diplophyllum albicans*, very abundant on acid soils, is characteristic.

Instead of disintegrating, as in the other two types of beechwood, the dead leaves of the litter, after being thoroughly wetted, become packed tightly together and gradually pass over below into a laminated raw humus (*mor*), sometimes an inch thick. Underlying this is mineral soil (*A* horizon) stained with humus above, while below is a narrow bleached layer, and then a very thin dark layer of humus material (*B* horizon) at a depth of not more than two or three inches from the surface. Here we have a definite though a very shallow podsol (see pp. 37-8). In spring the fine fibrous branches of the beech roots grow *upwards* into the layer of mor and dead leaves, and are soon infected by and thickly covered with mycorrhiza. The surface soil, which is quite destitute of earthworms, often becomes very dry in the summer and the surface beech roots may be all killed through lack of water.

The same general type of beechwood is found in various places on sands and gravels (which are often podsolised) in south-east England. In many of these the podsol structure is much more fully developed, the *B* horizon being well marked and formed at a greater depth. Two such beechwoods are well known to Londoners in Epping Forest and Burnham Beeches. Both of these are varied woodlands of great beauty, situated on low plateaux of Tertiary sands with overlying glacial gravels. They consist of birch, oak, and beech, with areas of open heath. Where the little streams have cut down to the underlying clay the woods are of the damp oak-hazel type, at Epping Forest with abundant hornbeams. The most familiar part of Burnham Beeches is that which is occupied by very old beeches with short thick trunks and spreading branches of no great height (Phot. 27). This habit is of course due to

original pollarding many years ago, i.e. cutting off the upper part of the tree while it is comparatively young. When pollarding is regularly practised the branches that spring from the top of the lopped trunk are cut at regular intervals, just as in coppicing the shoots from a stool are cut. If this is not done the branches of a pollarded tree go on growing and thickening, as they have done at Burnham Beeches, but the tree cannot grow very tall.

Below these old pollard beeches and wherever the shade is deep on the level stretches of the plateau the ground is bare of vegetation except for the great silvery-green cushions of *Leucobryum* (Phot. 26) with a few other mosses. The litter of beech leaves and the dead lower parts of the moss cushions pass into a thick resistant layer of mor above the acid gravelly mineral soil. On such ground there is no field layer, nor is any beech regeneration possible. Where the soil conditions are more favourable beech can regenerate and a small number of plants preferring or tolerating acid soil occur: bracken, wood soft-grass, wavy hair-grass, cow-wheat (*Melampyrum pratense*), small woodrush (*Luzula pilosa*), pill sedge (*Carex pilulifera*), wood sage (*Teucrium scorodonia*), wood violet (*Viola riviniana*). Of mosses and liverworts there are (besides *Leucobryum glaucum*) *Dicranum scoparium*, *Dicranella heteromalla*, *Polytrichum formosum*, *Diplophyllum albicans*, and a few others. Of the large fungi there are many species growing on the highly acid raw humus soils, and the following are characteristic: *Amanita mappa*, *Amanitopsis fulva*, *Boletus chrysenteron*, *B. edulis*, *Cortinarius elatior*, *Paxillus involutus*, *Russula fellea*, *R. lepida*, *R. ochroleuca*, *Scleroderma aurantium*—the Russulae, *Amanita*, *Paxillus*, and *Scleroderma*, particularly in acid sandy woods like Burnham Beeches, and the Boleti especially in the Chiltern plateau beechwoods on acid silty soils.

BEECH AND OAK

The English beechwoods give an exceptionally good opportunity of studying the development of the different types of wood—the succession of vegetation on different soils leading up to beechwood. We saw in the last chapter that stages in the succession to oakwood could be traced,

but partly because our beechwoods are on the whole in a more natural condition than the oakwoods, and also because, on some soils, beechwood follows oakwood in succession, there is here more ample scope for working out the stages of development. We owe almost all our knowledge of this subject to the thorough pioneer work of Dr. A. S. Watt.

The potential height-growth of beech and oak is about the same. On the best soils it substantially exceeds 100 feet: for exceptional individual trees heights of about 140 feet have been recorded. But beech casts a deeper shade than oak, and its shallow roots exploit the surface soil more thoroughly, leaving little water available for the young trees of other species. Oak cannot therefore easily establish itself under the shade of beech, while beech can do so among oak. It follows that on soils (and in climates) equally favourable to both trees beech under completely natural conditions will emerge triumphant and will form nearly pure woods. Why then, it will be asked, is there not beechwood rather than oakwood on a wider variety of soils which are quite favourable to beech in this country? The probable answer is that the preponderance of oak depends upon several factors, of which two may be mentioned. First of all, in our climate, oak produces abundance of acorns nearly every year, while good "mast years" when viable beech-nuts are produced in great quantity only occur at fairly long intervals. This presumably depends on climatic factors, of which late spring frosts, preventing "setting" of the nuts, and cool summers, checking their ripening, have been plausibly suggested. Beech-nuts seem more vulnerable to these factors than acorns. Secondly, the greater value of oak timber in past centuries, not to mention oak bark for tanning, has led to preservation and planting of oak rather than beech during the later stages of the progressive historical depletion of our natural woodlands.

To return to the differing conditions in which one or other of the two trees can succeed in natural competition. Beech cannot grow in waterlogged soil, and it seems that oak has a definite advantage on the heavier clays. On such soils, therefore, we never have natural beechwoods.

On the other hand, oak cannot make good trees on very shallow soils less than 12 inches in depth, and up to 20 inches or so oak is handicapped in competition with beech because it naturally forms a deep taproot, while the very plastic root system of beech can support a good tree when it is confined to surface soil. Thus we never get oakwoods on the very shallow soils of the chalk escarpments, which beech readily colonises. On the deeper loams covering the chalk plateaux, however, both trees can grow very well indeed, and here the superior competitive ability of beech enables it, if left alone, to form nearly pure beechwoods. But when these loams approximate to clays this superiority is reduced, because the soil conditions are apparently more favourable to the growth of oak. In some of the Chiltern plateau woods we find, in fact, beech and oak maintaining themselves side by side in the canopy; in others oak is dominant. But the general scarcity of beechwood and the frequent occurrence of oak-hazel wood, for example on the plateau clays and loams of the North Downs of Kent and Surrey, are probably due to former deliberate favouring and to some extent planting of oak.

On many of the sands of south-eastern England as a whole, beech and oak can grow equally well, though some are too dry for really good development of either tree, and birch and pine are the most successful (as they are always the first) colonists owing to the great quantities of their wind-carried seed. Where beech and oak can flourish, oak tends to come before beech, probably because of the greater abundance of acorns, but where there is a sufficient supply of mast, beech eventually establishes dominance.

CHALK SCRUB

The earliest stages of succession, before the establishment of trees, are quite different on these various soils. Succession to woodland begins when pasturage of grassland or heathland ceases. So long as a tract of land is heavily grazed or overrun by rabbits it is impossible for woody plants to establish themselves, but when grazing is withdrawn, rabbits not too numerous, and a supply of seed available, shrubs at once begin to colonise the area. On

R. J. Lythgoe

PHOT. 29. Dense juniper scrub on chalk escarpment invaded by white-beam, yew, and beech. Succession checked by rabbits. Chinnor Hill, Oxon.

R. J. Lythgoe

PHOT. 30. Chalk scrub near Wylye, Wilts. From left to right: yew, juniper, blackthorn, buckthorn, juniper.

R. J. Lythgoe

PHOT. 31. Juniper protecting privet (in fruit) and rose (right) in severely rabbit-eaten chalk grassland. Pulpit Hill, Bucks.

R. J. Lythgoe

PHOT. 32. Juniper protecting yew, buckthorn, holly, and rose. Near Figsbury Ring, Wilts.

the grassland of the chalk escarpment wild roses are often the pioneers, but the two principal shrub colonists are hawthorn and juniper, the former on the gentler slopes and deeper soils, the latter on the steeper slopes and shallower soils (Phot. 29). This difference of starting-point determines what may be regarded as two distinct successions or seres —the *hawthorn sere* and the *juniper sere*.

With increase in number of the bushes a more or less continuous scrub is formed, often containing a variety of other shrubs besides the two common dominants (Phot. 30). Dogwood (*Cornus sanguinea*), privet (*Ligustrum vulgare*), spindle (*Euonymus europaeus*), wayfaring tree (*Viburnum lantana*), buckthorn (*Rhamnus catharticus*) are the most characteristic, and hazel, elder, and field maple are also often present. Traveller's Joy (*Clematis vitalba*), more conspicuous and beautiful in fruit than in flower, is a very characteristic and abundant climber in chalk scrub. The light-loving grasses and herbs of the open chalk grassland are gradually killed out, so that the turf is destroyed and disintegrated as the scrub thickens and the shade increases. Around and between the shrubs many areas of semi-shade are created, and these are colonised by "marginal" woodland plants which flourish in open soil and in either fully lighted or half-shade conditions. Among them are the conspicuous grass *Brachypodium silvaticum* with its yellowish-green leaves and drooping shoots, the hairy violet (*Viola hirta*), ground ivy (*Nepeta hederacea*), ploughman's spikenard (*Inula conyza*), calamint (*Clinopodium vulgare*), the sweet-scented marjoram (*Origanum vulgare*), and sometimes the pale green fetid hellebore (*Helleborus foetidus*) or the deadly nightshade (*Atropa belladonna*). Most of them are calcicolous plants and all can grow in full light where they can get open soil, but most cannot establish themselves in close turf. Occasionally true woodland plants of deep shade are found under the shrubs, and of these the commonest is dog's mercury, which sometimes forms considerable sheets in such situations.

Tree saplings of various kinds frequently occur in the scrub, and they are often conspicuous in the middle of clumps of juniper, isolated in the middle of grazed pasture, the juniper protecting the saplings, and often also the less

formidable shrubs, from grazing and rabbit attack (Phots. 31, 32). The two most characteristic early tree colonists of chalk scrub are whitebeam (*Sorbus aria*) and yew (*Taxus baccata*), the former persisting, as we have seen, into the beechwood that is ultimately developed and the latter often recolonising it. Holly and gean, and occasionally other species, also occur in the scrub. Ash and beech are constantly found.

YEW WOODS

Owing to the very deep shade which it casts, excluding competition from other trees, and the persistence of individual trees to a great age (commonly 500 and up to 1000 years), yew established in chalk scrub may form, locally, small yew woods in the absence of general beech invasion. These are very numerous on the downs of West Sussex and the adjoining parts of Hampshire, the finest at Kingley Vale (Phots. 33 and 34), two miles north-west of Chichester. The yew woods are almost pure, with an occasional whitebeam surviving from the scrub, and cast such a deep shade that practically nothing grows beneath them (Phots. 35, 36); but dead remains of scrub are sometimes found, showing that the yew started in chalk scrub. The yew woods are practically confined to the heads of small dry valleys in the chalk, and to slopes running from south-west to north-east where scrub has become established under the lee of an advancing beechwood. In both these situations the scrub and the succeeding yew get good protection from wind.

SUCCESSION TO BEECHWOOD

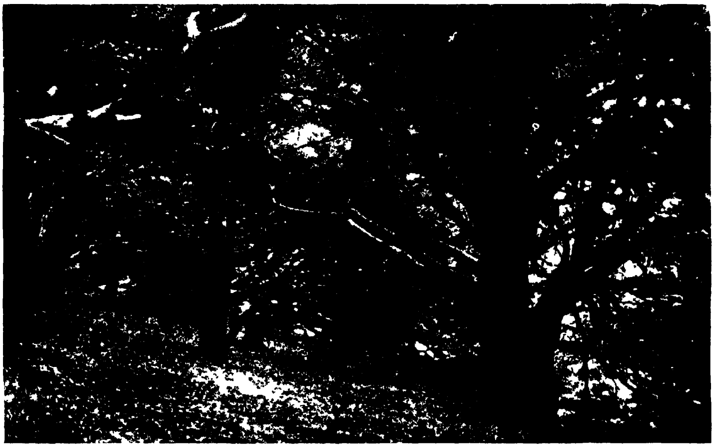
Ash occurs everywhere in chalk scrub, though it is not abundant on the Chilterns, and where conditions are favourable, as on the South Downs, it increases so as to convert the scrub into a young ashwood, but (apart from the intervention of yew) ash is ultimately overtaken by beech if enough seed parents exist in the neighbourhood. Beech migrates and develops much more slowly than ash, so that the latter gets a good start, but since beech steadily invades both scrub and young ashwood and casts a shade which the light-loving ash cannot tolerate, it emerges triumphant in the end.

R. J. Lythgoe

PHOT. 33. Yew wood at the head of Kingley Vale, near Chichester, with yew-ash wood on the left.

R. J. Lythgoe

PHOT. 34. Continuation to the left of Phot. 33, with yew wood and yew scrub. The white trees in the yew woods are whitebeams.



Uehlinger

PHOT. 35. Interior of old yew wood at the head of Kingley Vale. The ground is bare. Oldest yews, 500 years.

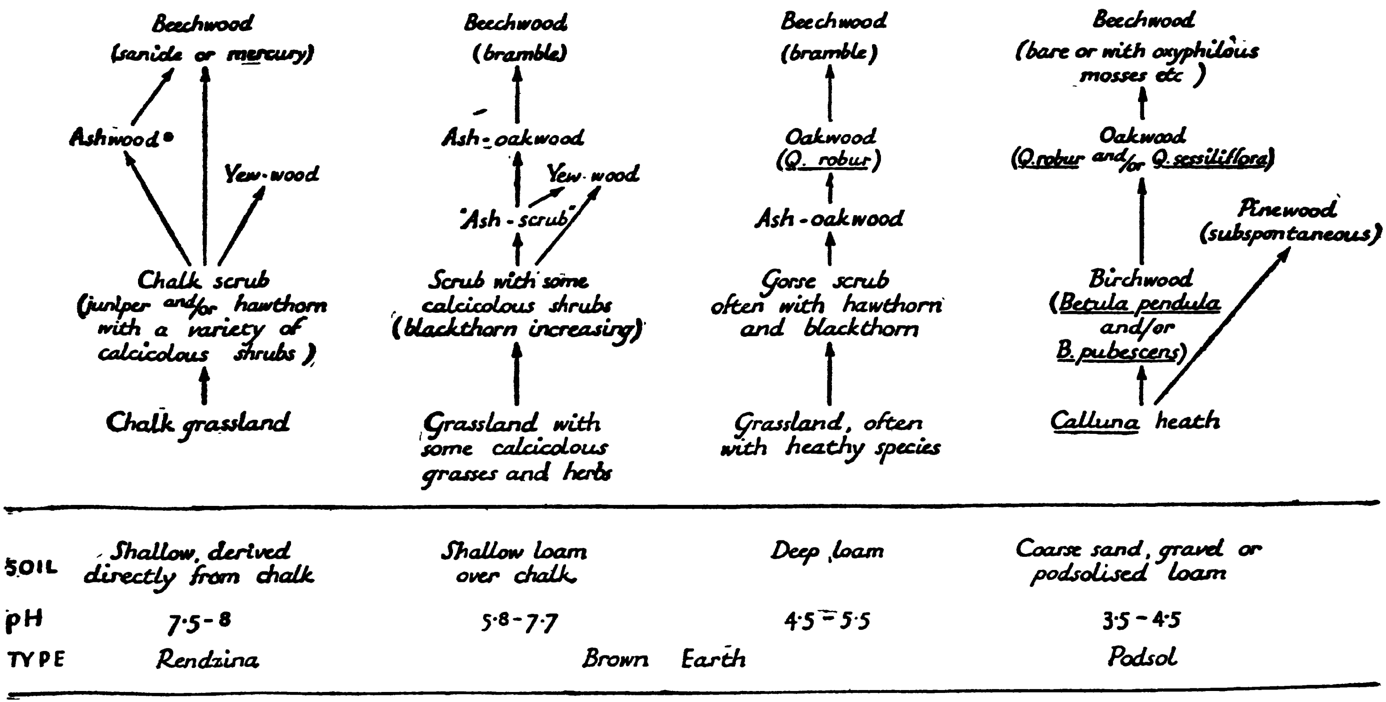
Uehlinger

PHOT. 36. An old yew from the wood, over 20 ft. in girth.

Face p. 113

On the steep slopes of the Chiltern escarpment where juniper dominates the scrub, and ash is scarce, beech directly colonises the scrub, and as soon as it begins to cast shade the juniper begins to die. In the young beechwoods so formed dead juniper bushes are commonly seen. While in the hawthorn sere of the South Downs there is usually succession from scrub through ashwood to beechwood, in the juniper sere the succession thus often goes directly from scrub to beechwood (Phot. 29).

On the loams, clays, and silts of the chalk plateaux the course of succession is more varied because of the varied soils on which it takes place, but we may consider chiefly the "central" type of plateau soil, often a rather acid loam which is deep and fertile, being rich in nutritive mineral elements, and which ultimately bears the finest beechwoods (Phot. 28). The pastured grassland from which this succession starts, on withdrawal or great diminution of grazing, is of "neutral" or somewhat acid type (see Chapter IX), and is invaded by heather and bracken, and also by various shrubs, of which gorse, hawthorn, and blackthorn are the commonest, so that local patches of scrub are formed. Various trees invade the heather areas, but especially the scrub, and of these oaks are by far the most numerous and successful, though beech and ash are also well represented. This colonisation results in the formation of ash-oak wood, since ash reproduces itself more quickly than oak, and beech much more slowly, so that beech remains as isolated trees and in small "families" for a long time. As soon as woodland cover is established, bramble and honeysuckle come in and form something like a continuous upper field layer, while a considerable variety of woodland herbs appears, including some "exacting" species, i.e. those requiring a fertile soil, like sweet woodruff, mercury, and sanicle; others which are "tolerant" species, such as wood-sorrel and bracken; and others again which affect the more acid soils, such as sweet vernal grass (*Anthoxanthum*), earth nut (*Conopodium denudatum*), foxglove, tormentil, and bluebell. Shrubs, including hazel, guelder rose, and privet, with holly and ivy, also become prominent, and ash recedes, leading to the formation of an oakwood stage which is, however, being progressively invaded by beech. The



A. S. Watt.

FIG. 2. Successions in south-eastern England from grassland and heath to climax beechwood of various types depending on different soils.

first effect of the spread of beech in the wood is to reduce the number of species and individuals in the shrub and field layers, and when the beech canopy becomes continuous the lower layers of vegetation practically disappear and the wood is a "one-layered" community. After half a century or so the canopy begins to open out and herbs, with a very few shrubs, begin to come in. The bare stage is succeeded by the dominance of woodsorrel (*Oxalis*) in the field layer, and this lasts a few years and is followed by bramble (*Rubus*), whose dominance in the field layer apparently persists indefinitely.

On the somewhat calcareous loams the succession to beechwood takes a course intermediate between that just described and that which occurs on the chalk escarpments. The grassland contains more calcicolous grasses and herbs, heather and bracken are absent; in the scrub stage gorse is absent, and besides hawthorn and blackthorn there are more calcicolous shrubs. Ash comes in earlier and oak is less prominent, with no oakwood phase. In the final beechwood the "bare" stage lasts much longer, bramble and woodsorrel not appearing for more than a century and never becoming dominant, while the field layer contains more of the escarpment woodland plants and no species of acid soils.

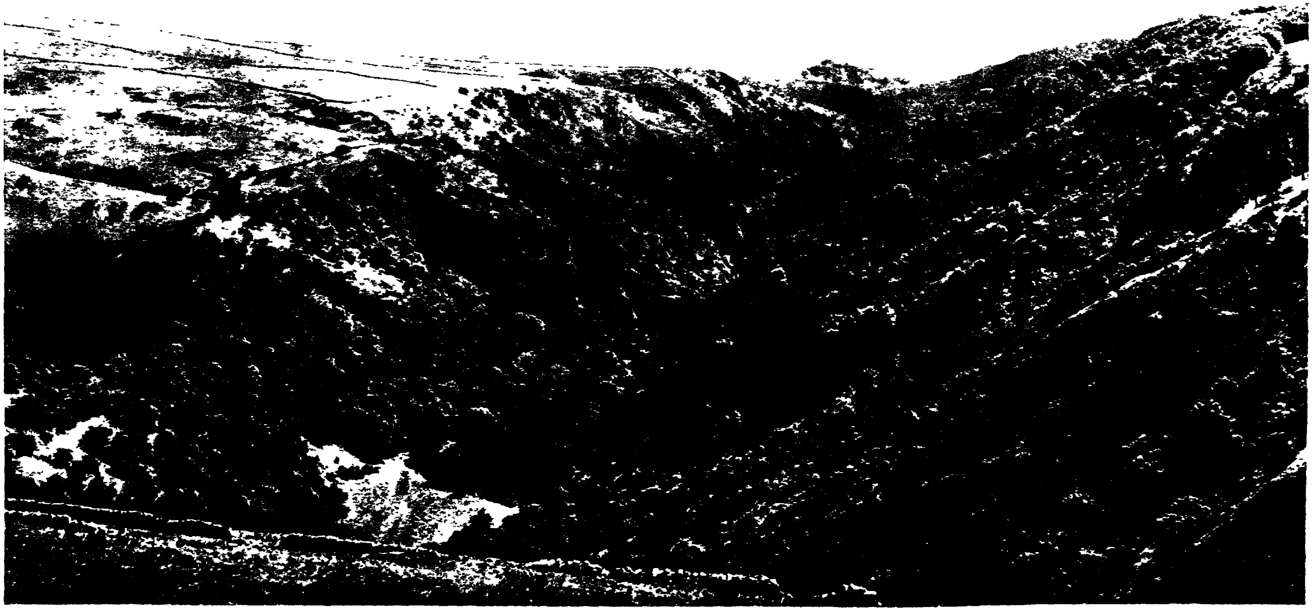
On the acid sands, for example at Burnham Beeches, the succession is quite different. It starts with heath (or grass heath if the area has been heavily pastured). This is invaded by birch, and by pine if there are mature pines in the neighbourhood to furnish seed. If the pines are abundant enough a pinewood is formed (see p. 128); if not, a loose birchwood with heather and other heath plants persisting between the birches, which cast but little shade. Shrubs are not prominent. Oaks follow the birches, either the sessile or the pedunculate oak, or both together. The oakwood so formed has a heath field layer, and may hold the ground indefinitely, but when there is plenty of beech in the neighbourhood this tree enters the wood, and may ultimately dominate it, as at Burnham Beeches. Ash, hazel, and field maple are quite absent from the succession, as well, of course, as the calcicolous shrubs.

Fig. 2 shows diagrammatically the phases of these

various successions, all culminating in beechwoods, but beechwoods of very different types.

SCOTTISH BEECHWOODS

Although natural beechwoods are confined to the south of England, beech can grow quite well and set viable seed in suitable places as far north as eastern and even northern Scotland. In eastern Aberdeenshire, indeed, the seed from planted trees actually colonises the ground and forms woods in favourable places. Some of these are on good fertile loams and their vegetation resembles that of the good loams of the chalk plateaux, though with certain differences. Others are on podsols and resemble the southern sandy beechwoods with a field layer of bilberry (Phot. 28, p. 107). It is doubtful, however, if beechwood could maintain itself indefinitely on these northern podsols.



W. J. B. Blake

PHOT. 37. Ashwood lining the sides of Dovedale, Derbyshire.

W. M. Rankin

PHOT. 38. Ash trees have sown themselves in the fissures of a limestone pavement and will develop a closed ashwood. The surface of the pavement has become covered with vegetation which will develop into the field layer of the wood Chapel-le-Dale, W. Yorkshire. Ash in flower, April.

CHAPTER VIII

ASH, ALDER, PINE, AND BIRCH WOODS

Scrub Vegetation

ASHWOOD

THE growth of ash is good on calcareous soil (p. 72), and on the shallow soil of the chalk escarpments, as we have seen, ashwood is found as a stage in the development of woody vegetation which culminates in beechwood (p. 112). Outside the region where beech is aggressive and dominant as a wood-forming tree ash forms the climax woodland on limestone soils. This is seen most conspicuously in the Derbyshire dales (southern Pennines), where considerable tracts of natural or semi-natural ashwood still exist on the sides of the deep valleys in the Mountain Limestone (Phot. 37). These woods are developed largely on the screes formed from fragments of limestone fallen from the crags. Smaller ones occur on the same geological formation of the northern Pennines in the West Riding of Yorkshire, and also on limestones of the Yoredale series in the same region. Apart from the woods on the valley-sides, where the beds of Mountain Limestone are horizontal, they often form flat "pavements" with deep fissures between the blocks, and in these fissures ashes may sow themselves, and growing up, convert the "pavement" into an ashwood, the level floor between the fissures ultimately becoming covered with humus in which a typical ashwood flora develops. Woodland plants in considerable variety actually settle in the fissures, where they find moisture and shade, before the trees develop. Photograph 38 shows an ashwood developing on a limestone pavement. Other areas of Mountain Limestone—at low levels near the sea in north Lancashire, in North Wales, and on the Mendip Hills in Somerset (Phot. 39)—also bear fragments of ashwood, and the same is true of various limestones of different geological for-

mations and of other calcareous soils, such as calcareous Upper Greensand (Phot. 41) in different parts of the country. Wherever, in fact, limestone soils occur, there we have—outside the beech region—ash as the natural dominant tree. Within the region where beech is dominant, ash usually precedes it in the woodland succession on limestone soils. A good example of such a "seral" ashwood with calcicolous shrubs, is shown in Photograph 42 from the oolitic limestone escarpment of the Cotswold Hills. Where calcareous soil is deep, however, oak comes into the woods and we get transitions to the ash-oak woods described on p. 86.

Ashwoods quite similar to these on limestones also occur on "basic" igneous rocks, i.e. rocks containing alkaline salts besides those of calcium and yielding a shallow soil rich in nutritive mineral elements. An example of an upland ashwood on basic igneous rock is shown in Photograph 40.

Of trees accompanying the ash, wych elm (*Ulmus glabra*) is characteristic and frequent, much more so than in oakwoods; in the south also yew and whitebeam (as in beechwoods), in the north bird-cherry (*Prunus padus*). Aspen and field maple are often present, but the birches are usually quite absent. In some ashwoods or ash-oak woods, however, the silver birch (*Betula pendula*) is frequent, and at the highest altitudes hairy birch (*B. pubescens*)—which is not always hairy!—with mountain ash (*Sorbus aucuparia*). The small-leaved lime (*Tilia cordata*) occurs in some limestone woods in the west of England and in Wales.

Owing to the openness of ash foliage plenty of light penetrates the canopy of an ashwood, and this fact, combined with the favourable effect of lime in the soil, leads to a rich development of the shrub and field layers, including not only a great number of species occurring in the oakwoods, but also many calcicolous species which are not found there. Hazel is often the dominant shrub, hawthorn is usually abundant, and blackthorn is also common. Some or all of the calcicolous shrubs already described as characteristic of chalk scrub and of ash-oak wood on calcareous soil—dogwood, spindle, privet, buckthorn, elder, wayfaring tree—are often abundant in ashwoods of the south, but in the north their frequency is much less and

ASHWOODS ON LIMESTONE AND OTHER BASIC ROCK

W. B. Crump

PHOT. 39. Ash-hawthorn scrub and ashwood on Mountain Limestone Ebbor Gorge, Mendip Hills, Somerset.

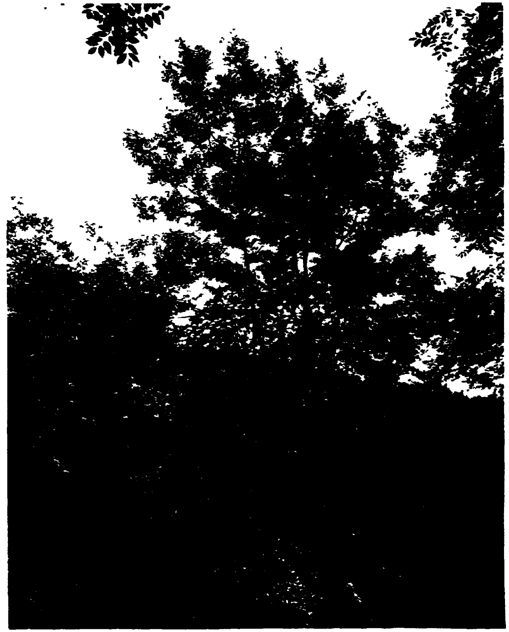
E. Price Evans

PHOT. 40. Upland ashwood at about 1000 ft. on scree and rock of basic volcanic beds at Craig-y-Benglog near Dolgelly.

Face p. 118

R. J. Lythgoe

PHOT. 41. Ashwood on calcareous Upper Greensand in a south-east Devon valley. Watercombe Wood, Branscombe, S. Devon. April.



C. G. P. Laidlaw

PHOT. 42. Ashwood on Oolitic Limestone, Cotswold Hills, Witcombe Wood, Glos. June.

some of them are absent. Traveller's joy (*Clematis vitalba*), the characteristic and abundant climber of calcicolous scrub in the south, is absent in the north. Ivy, on the other hand, is very common, but honeysuckle is not.

In the field layer there are a number of societies formed by gregarious species. On the driest soils, such as those of partially weathered limestone screes on which ashwood has developed, ground ivy (*Nepeta hederacea*) often forms small societies, and others may be dominated by wood sage (*Teucrium scorodonia*) or by hairy St. Johnswort (*Hypericum hirsutum*)—a characteristic calcicole. Lily-of-the-valley (*Convallaria majalis*) and stone bramble (*Rubus saxatilis*) also form local societies in dry places. On somewhat less dry soils societies of dog's mercury—a plant which is far commoner on, though, as we have seen, by no means confined to, calcareous soils—are widespread, and with it is often associated the moschatel (*Adoxa moschatellina*), whose delicate prevernal leaves and the heads of little yellowish-green flowers set back to back find shelter among the robust and vigorous shoots of the mercury.

On soils of medium moisture societies of lesser celandine (*Ficaria verna*) and bear's garlic or ramsons (*Allium ursinum*) often occur, and there is a rich accompanying flora which includes many common species of damp oakwoods and the following more interesting species, several of which we have already seen to be characteristic of beechwoods: columbine (*Aquilegia vulgaris*), cuckoo-pint or lords-and-ladies (*Arum maculatum*), sweet woodruff (*Asperula odorata*), great bell-flower (*Campanula latifolia*), water avens (*Geum rivale*), wood forget-me-not (*Myosotis silvatica*), butterfly orchid (*Platanthera chlorantha*), and in the north Jacob's ladder or Greek valerian (*Polemonium caeruleum*) and globe-flower (*Trollius europaeus*). Several of these are rarely, if ever, found in oakwoods of the same regions, and that may also be said of the handsome bloody cranesbill (*Geranium sanguineum*), a kind of St. Johnswort (*Hypericum montanum*) and the green hellebore (*Helleborus viridis*). A very rare plant found in some northern ashwoods is the baneberry (*Actaea spicata*).

In woodland marshes by the sides of streams and round springs, in or on the edges of woods, a number of species

of wet soil occur, but none of these seems to be specially characteristic of calcareous soil. Calcicolous marsh plants do exist, but they are not woodland plants.

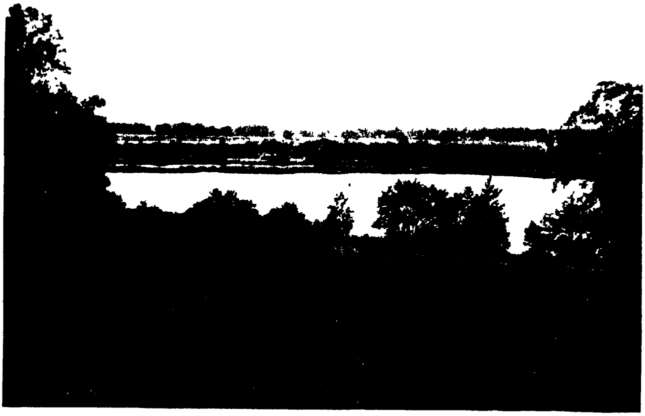
A number of mosses and liverworts are found in the ash-woods, though not so many as in the oakwoods. Some of the abundant species, e.g. *Hypnum molluscum* and *Mnium rostratum*, are practically confined to calcareous soils.

Where ashwood is developed on basic igneous rocks, its characters strongly resemble those of typical limestone ash-wood. These woods contain a mixture of calcicolous, exacting, and indifferent plants, but with some few species of acid soils, probably dependent on thorough leaching under high rainfall with accumulation of acid humus.

The ashwoods of the limestone valley-sides, as we have seen, are mainly developed on the screes or talus which has accumulated at the foot of cliffs forming the walls of the original gorge cut out of the rock by the action of water. The fallen blocks gradually weather down to form a fine soil, and it is in this that the pioneer flowering plants settle, while the rocks themselves become coated with lichens and mosses. Shrubs—hazel and hawthorn in greatest numbers—take root in the gaps between the boulders, into which loose soil has washed, and these are joined by young ashes. Thus the first vegetation of the screes, consisting of lichens and mosses and those flowering plants which can live in the raw dry limestone soil, is gradually replaced by hawthorn or hazel scrub and then by ashwood as the trees grow up. As humus accumulates and makes the soil more favourable a wider variety of woodland plants is able to colonise the young wood, till the rich flora of the mature wood is developed.

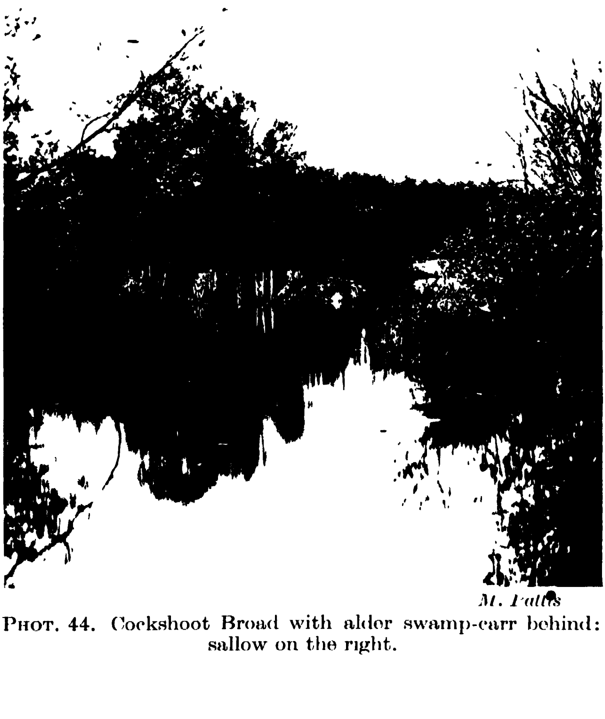
ALDERWOOD

Alderwood naturally develops on waterlogged soil which is not too acid or too poor in nutritive mineral elements. Thus it is found in alluvial marshes and in peat fens, but not in bogs: also on the low banks of lakes and ponds, rivers and brooks, where the roots can easily reach soil that is more or less constantly wet. There is no doubt that in prehistoric "Atlantic" times, and in the early historical



F. F. Blackman

PHOT. 43. Salhouse Broad, River Bure and Hoveton Broad seen from the upland. Alder carr on the broad strip of peat between the river and Hoveton Broad.



M. Pallis

PHOT. 44. Cockshoot Broad with alder swamp-carr behind: sallow on the right.

EAST NORFOLK ALDER CARRS

J. Massart

PHOT. 45. Alder swamp-carr with tall sedges in front. Rockland Broad.

J. Massart

PHOT. 46 Heron's Carr, Barton Broad. Alder and hop.

J. Massart

PHOT. 47. Heron's Carr. Alder and hemp agrimony.

Face p. 121

("Sub-Atlantic") period, alder was much more abundant in the oakwoods, while alderwood must have occupied much of the very extensive low-lying alluvial soil. But with the progress of draining and clearance for cultivation these extensive alderwoods gradually disappeared, and there remain only fragments on still undrained ground.

The alderwoods on the margins of the "broads" and on the fens of east Norfolk (Phots. 43-47), though now of small extent, are largely still in a very natural unspoiled condition. Some indeed have all the characters of "virgin forest," since they are practically untouched and show a tangle of vegetation with trees of all ages, old decaying trunks remaining *in situ*, rotting logs and branches on the ground, and saplings growing up between. These woods are locally known as *carrs* (connected with the Icelandic word *kjarr*, a fenwood). In Yorkshire and Lincolnshire the same word "carr" is applied to any tract of fenland (Swedish *kaerr*). The air of these carrs is constantly very moist, because of the saturated soil and the frequency of standing water, in spite of the low rainfall of the district (under 25 inches). The water vapour arising from the swampy soil is not dispersed by wind in the shelter of the wood; and not only the dead wood lying on the ground but also the bark of the tree trunks and the branches and twigs are covered with mosses and lichens.

Accompanying the dominant alder (*Alnus glutinosa*), ash and hairy birch (*Betula pubescens*) are the commonest trees, and of shrubs grey sallow (*Salix atrocinerea*), buckthorn (*Rhamnus catharticus*), alder buckthorn (*Frangula alnus*) and guelder rose (*Viburnum opulus*). Pedunculate oak (*Quercus robur*) commonly invades the alder carr later on. Other shrubs are hawthorn, privet, and spindle. The marked representation of calcicolous shrubs is interesting and presumably due to the large amount of lime in the ground water of typical fen which drains from the chalk. Very characteristic of these fen woods are the three species of *Ribes*: black currant (*Ribes nigrum*), red currant (*R. rubrum*), and gooseberry (*R. grossularia*). Characteristic also are the climbers: great bindweed (*Calystegia sepium*), hop (*Humulus lupulus*, Phot. 46), and bitter-sweet or woody nightshade (*Solanum dulcamara*). Ivy is also common.

The field layer is equally characteristic. The most distinctive species are fen fern (*Dryopteris thelypteris*), the great stooled sedge (*Carex paniculata*) and other sedges, yellow flag (*Iris pseudacorus*), stinging nettle (*Urtica dioica*), meadow-sweet (*Filipendula ulmaria*), comfrey (*Symphytum officinale*), hemp agrimony (*Eupatorium cannabinum*, Phot. 47). With these are many other marsh plants which grow in saturated soil and can tolerate the shade of the carr. Many of the field-layer plants, for example the iris, meadow-sweet, and comfrey, do not flower in the shade of alder carr, though their vegetative growth is vigorous enough. Many of the common mosses and liverworts that grow in other woods are found also in the carrs, and besides these there are some which usually grow in very wet places or even under water, such as *Amblystegium filicinum* and *Hypnum riparium*.

Carr develops on the peat formed by the reedswamp and fen on the margins of the broads and rivers (see Chapter XIV). Grey sallow is one of the first colonists, and with alder buckthorn, common buckthorn, and guelder rose forms a scrub which is soon invaded by alder. Ash and birch may also appear early (Phot. 114, p. 226). Oak appears later and, together with birch, consolidates the peat with its root system, overshadows the shrubs and other trees, and may convert the carr into wet oakwood. The appearance of these different trees depends, of course, on the presence of seed parents in the neighbourhood. Thus in Cambridgeshire isolated areas of fen surrounded by arable land do not contain alder at all and the carr remains in the scrub stage (cf. Phot. 118, p. 226). In wide areas of fen where there are no oaks in the vicinity and the water level remains high, pure alder carr apparently maintains itself indefinitely.

Fragments of alderwood occur all over the country in marshy areas which have escaped drainage, but they are steadily decreasing in number. The great stools of *Carex paniculata* are a characteristic feature of these untouched alderwoods. At one time alder was preserved and planted for the making of gunpowder from its charcoal, and in the north for making clogs.

PINEWOOD AND BIRCHWOOD

Pinewoods and birchwoods may be considered together, for the common pine ("Scotch fir") and either or both of the two British species of birch very often grow together because they make similar demands on climate and soil. Both trees produce abundant pollen (pine more than birch) and abundant seed (birch more than pine). Pollen and seed are alike distributed by the wind, but the one-seeded birch fruits are smaller and lighter as well as more numerous than pine seeds, so that they can colonise the ground in greater numbers over wider areas. Both trees are very tolerant, flourishing in cold temperate and subarctic climates, but some kinds of birch go farther north in the arctic than pine, forming the most northerly tree belt in Lappland, and correspondingly higher on the hills. Both can grow on a wide range of soils extending to the poorest and most acid, where indeed they are often almost the only trees present. Pine can grow well on dry calcareous soils, while birches usually avoid them, though silver birch (*Betula pendula*), which is somewhat more exacting than *B. pubescens*, sometimes occurs in woods on calcareous soil. On the other hand, the hairy birch (*B. pubescens*) can grow on wetter soils than pine and is often an important constituent of fen and marsh woods.

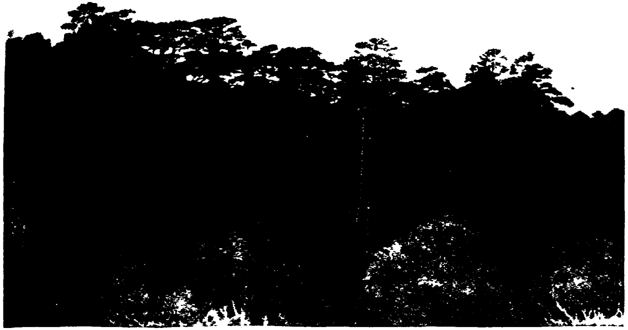
The abundance and ease of distribution of their seed, their tolerance of poor light soils, and their quick growth, make pine and birch pre-eminent pioneer colonists in our latitudes, and mass invaders of heathland, where pine and birch wood may become established before the heavier-seeded, slower-moving oak and beech are represented by more than a few isolated young trees. Such local pinewoods on heathland persist for a long time, and owing to the deep shade which they cast it is doubtful if they would be displaced by any other form of woodland. Birchwood, on the other hand, casts very light shade and is easily superseded by oak or beech. In the Scottish Highlands, however, where beech is not native and oak occupies only the better soils towards the bottoms of the larger valleys, birch and pine do not have to face these competitors, and

here we have the scanty remains of the birch and pine forests which occupied most of Britain in Boreal times.

The common European pine (*Pinus silvestris*), known in England traditionally as "Scotch fir" and now often called "Scots pine," was the most important dominant of the Boreal forests. With the beginning of the Atlantic period it receded in numbers, advanced again in Sub-Boreal times, and then receded afresh. In some places its pollen is present at all levels in the peat right up to the present day, the grains in the uppermost layers coming from planted trees. Small groups of pines or single trees are found in most parts of the country in more or less "wild" situations, and until quite recently they were taken to be either themselves planted or the offspring of planted trees.[1] But though many of these sporadic pines have certainly had such an origin, it has become probable, since more continuous pollen records from peat have been available, that some may well be descendants of native trees. There was a great deal of pine planting in southern England as well as in Scotland in the eighteenth and nineteenth centuries, and many of the numerous "subspontaneous" pinewoods on the southern sands are certainly due to wholesale colonisation of heathland by seed from mature pines planted on neighbouring estates. It is remarkable that pine reproduces itself and regenerates pinewood most freely on these southern sands and in some of the old native pinewoods of the Scottish Highlands, rather than in the intermediate regions of northern England and southern Scotland. This may be due simply to the difference in abundance of seed parents.

The Highland pinewoods are now but poor remnants of what they were even half a century ago, though their wholesale destruction began as far back as the seventeenth century. It is impossible to say just what their original distribution was, but, broadly speaking, they probably occupied a position between the oakwoods of the bottoms and lower slopes of the larger glens and a fringe of birchwood on the highest slopes which trees could inhabit, as well as covering great areas of glacial (morainic) gravel on

[1] The self-sown offspring of planted trees are generally called "subspontaneous,"—an ugly word.



PHOT. 48. Well-grown pines about 70 ft. high in Ballochbuie Forest, Aberdeenshire. Birches in the valley in front. Alt. 1200 ft.

A. G. T.

PHOT. 49. Stand of well-grown pine in close canopy with heather and cowberry in field layer, Ballochbuie Forest.

A. G. T.

PHOT. 50. Close stand of young pine in Rothiemurchus Forest, Inverness-shire, with cowberry and bilberry below and heather in well-lighted foreground.

A. G. T.

A. G. T.

PHOT. 51. Pines at 1650 ft. alt. above Lochan Eilein, Rothiemurchus Forest. Some of the trees are suffering or dead. Heather, bilberry, cowberry, crowberry.

A. G. T.

PHOT. 52. Free pine regeneration near Loch Maree. Young pines of various ages are seen round the old tree in the centre. Bracken and heather.

A. G. T.

PHOT. 53. Invasion of heath by young pines from pinewood behind. Hook Common, Surrey.

flatter ground. Only on the southern edge of Rothiemurchus Forest in Inverness-shire does pine now reach the present altitudinal limit of tree-growth—about 2000 feet—and towards this altitude the trees are often distorted or moribund (Phot. 51). Over much of the Highlands widespread sheep-grazing has prevented and still prevents regeneration of such pine as remains here and there; and after the great Highland sheep industry declined in the nineteenth century and was replaced by the formation of vast "deer forests" on the mountains and moors, the excessive numbers of red deer which were preserved for stalking carried on the destruction of seedlings and saplings, which steadily diminishes both pine and birchwood. Added to these causes of destruction, considerable areas of native pinewood were cleared during the war of 1914-18, and within the last twenty-five years the Forestry Commission, in its zeal for planting foreign conifers, has felled a good deal of fine native pine which had survived until then.

Two tracts of native pinewood which are still regenerating naturally are parts of Rothiemurchus Forest (Phot. 50) at the foot of the Cairngorm Mountains in the eastern Highlands and a small area (Phot. 52) on the southern shore of Loch Maree in Ross-shire (north-western Highlands). Other old native pinewoods are Ballochbuie Forest (Phots. 48, 49), belonging to the King, on Deeside in Aberdeenshire at the foot of Lochnagar, and the Black Wood of Rannoch at the foot of Schiehallion in the central Highlands of Perthshire. All four of these are situated at about 1000 feet on light gravelly morainic soil at the foot of mountain masses, and this habitat seems to furnish the best conditions for regeneration, though Ballochbuie does not regenerate well, probably owing to the attacks of deer.

Accompanying trees are only occasional. Birch and rowan (mountain ash) are the commonest, and sometimes aspen or alder are seen, but the pine forest is nearly always relatively very pure. Shrubs are practically absent, apart from the ericaceous undershrubs which form the field layer; but juniper (*Juniperus communis*) occurs in open places where full light has access. The thick field layer is typically dominated by bilberry (*Vaccinium myrtillus*),

called "blaeberry" in Scotland, and cowberry (*Vaccinium vitis idaea*), with heather (*Calluna vulgaris*) where there is enough light (Phots. 49, 50). Towards the upper limits of pine forest bearberry (*Arctostaphylos uva ursi*) and crowberry (*Empetrum nigrum*) are associated with the heather and Vaccinia. Bracken is very local, while hard fern (*Blechnum spicant*) is frequent. There are a few herbaceous plants among the heath undershrubs, but none is abundant. The commonest are wavy hair-grass (*Deschampsia flexuosa*), heath bedstraw (*Galium saxatile*), and tormentil (*Potentilla erecta*)—three species universally found throughout the country on sandy and gravelly acid soils. Besides these there are a number of relatively rare species more or less characteristic of pinewoods. One of these is chickweed-wintergreen (*Trientalis europaea*), with white 5-6-lobed flowers and a single whorl of leaves below. This is a northern plant, quite abundant in many of the Highland birchwoods, but not found in the south. Others are the wintergreens (*Pirola*), allied to the heaths, with evergreen leaves and elegant white, pink, or yellowish flowers—*Pirola minor* (the commonest), *P. media*, *P. rotundifolia*, *P. secunda*, and *Moneses uniflora*; *Linnaea borealis*, with small pink flowers in pairs, common in Scandinavia and parts of the Alps; and three orchids—lesser twayblade (*Listera cordata*), coral root (*Corallorhiza trifida*), and *Goodyera repens*. The last two and *Moneses* are said to be confined to old pine forests, and all are somewhat rare or very rare acid humus plants.

Where the heath layer is dense and continuous there is little possibility of anything growing among or beneath it, but where it is less thick there is a well-developed moss layer with species of *Hylocomium* (*H. splendens*, *H. triquetrum*, and *H. loreum* co-dominant), *Hypnum schreberi*, and *Hypnum crista castrensis* among the most characteristic species, and species of bog moss (*Sphagnum*) and *Polytrichum commune* in wet places.

The dominants of the field and moss layers of old pinewood are often practically the same as in the vegetation of the open heath outside the woods. The bilberry and cowberry flourish equally well in full illumination. Heather does better and only flowers freely in the open, while it is

excluded in the deeper shade. The mosses flourish in the partial shade of the undershrubs on the open heath. Thus the field and ground layers of pinewood are largely independent of the presence or absence of the trees, and the adjoining heaths often represent areas from which pinewood has disappeared. Some, though not all, of the rare characteristic pinewood plants mentioned above are, however, shade species and only met with in the woods themselves.

While there is no birch in closed pinewood because it cannot live in the shade of pine, the two constantly grow side by side in groups or as isolated trees, and birch may fill up gaps in pinewood just as it does in oakwood. Continuous birchwood (Phots. 54, 55) occurs farther north, and on the whole reaches higher altitudes, than pinewood and is now much more widespread in Scotland, though the individual woods are relatively small and often degenerate owing to sheep-grazing and the attacks of deer. The birchwoods inhabit a wide range of soils, but are usually found on more compact, finer-grained soils than the coarse sands and gravels of most of the still existing native pinewoods. Correspondingly they frequently develop a grassy vegetation which is grazed by sheep, while in the heathy vegetation of the pinewoods there is little to eat. Such birchwoods often form the upper fringe of oakwoods occupying the bottoms and lower slopes of the valleys, and their flora is an impoverished oakwood flora.

The silver birch (*Betula pendula*), with glistening white bark, occurs and sometimes forms woods in the southern Highlands, but most of the Highland birchwoods consist either of some form of the very variable hairy birch (*Betula pubescens*), usually with browner bark, or of certain northern forms probably belonging to one or more distinct species which have never been properly described and named. By far the commonest accompanying tree is mountain ash or rowan (*Sorbus aucuparia*), nearly always present, though often in small numbers. Rowan, whose seeds are distributed by birds which eat the bright red berry-like fruits, is very resistant to wind, and one is always coming across isolated stunted rowans on the moors, sometimes at higher altitudes than are reached by any

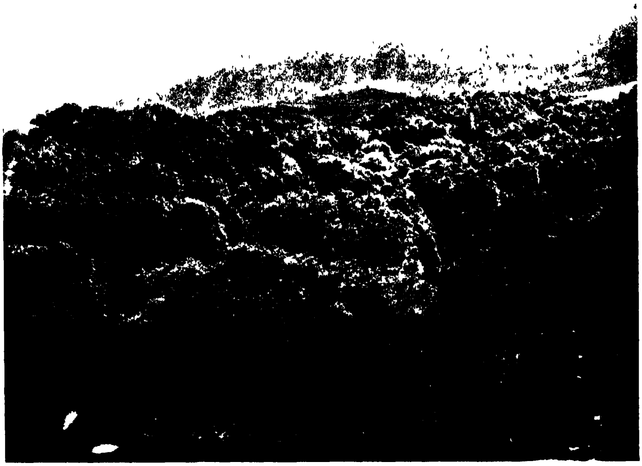
other tree. On the better soils aspen forms local societies, in the wetter places alder, while bird-cherry (*Prunus padus*) is occasionally found. Of shrubs the sallows, especially *Salix aurita*, are fairly common, and on the better soils hazel forms thickets. Both ivy and honeysuckle occur.

The field layer is very various according to the soil. On the better soils at the lower altitudes may be found primrose, bluebell, wild strawberry, stitchwort, self-heal (*Prunella*), germander speedwell (*Veronica chamaedrys*), red campion (*Melandrium dioicum*), wood pimpernel (*Lysimachia nemorum*)—all oakwood plants—as well as grasses: common bent (*Agrostis tenuis*), red fescue, rough-stalked meadow-grass (*Poa trivialis*), cocksfoot (*Dactylis*), and *Brachypodium silvaticum*. Many of the woods, however, have a field layer of bracken, and others of bilberry and heather, and in these we have the usual plants accompanying the heaths—wavy hair-grass, tormentil, heath bedstraw, wood sage, and so on. The birchwood flora includes two or three northern plants not found at all in the south —the hairy bugle (*Ajuga pyramidalis*), lesser twayblade (*Listera cordata*), and chickweed-wintergreen (*Trientalis europaea*), of which the last is much the commonest.

The mosses are very much the same as in the pinewoods —the Hylocomia, *Hypnum schreberi*, *Plagiothecium undulatum*, etc.

The "subspontaneous" pinewoods of the southern sands have already been mentioned. They are formed by colonisation of heathland by pine seed blown from neighbouring plantations or from already established subspontaneous woods (Phot. 58). The only check to the spread of pine is extensive felling, as in the two recent wars, and occasional heath fires, which often occur in dry summers.

The shade cast by the pines, though not so deep as that of old coppice or of young beechwood, is fairly heavy, as well as being continuous throughout the year; and this, with the thick layer of dead pine needles which remain undecayed for a long time in the relatively dry climate, prevents the development of any general field layer such as we get in the Highland pinewoods. Small beech and oak shrubs, often flat-topped and with thin leaves owing to their development in continuous deep shade, occur here



A. G. T.

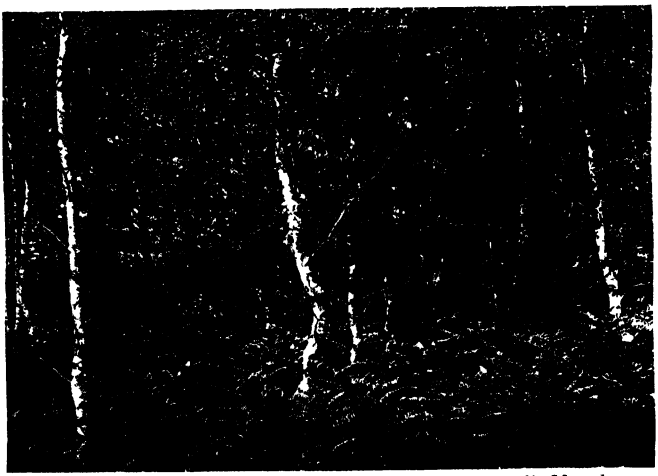
PHOT. 54. Birchwood near Kinloch Rannoch, Perthshire, 900–1250 feet.

A. S. Watt

PHOT. 55. Birchwood on the shore of Loch Shin, Sutherlandshire. Bracken, woodsorrel, common bent grass in field layer.

A. G. T.

PHOT. 56. Birchwood at Hesworth Common, Fittleworth, Sussex, with scattered birches on the heath in front.



S. Mangham

PHOT. 57. Dense young birchwood at Pressridge Warren, Sussex. Bracken in well-lighted foreground.

c

and there in these woods, doubtless overtaken when quite young by the growth of the overshadowing pines. Locally sycamore (*Acer pseudoplatanus*) or sweet chestnut (*Castanea sativa*) may appear as similar shrubs. Where the pine-needle litter is not too thick the bilberry and wavy hair-grass may be found, and also a number of mosses characteristic of acid soils, for example *Campylopus flexuosus, Dicranella heteromalla, Hypnum schreberi,* and the characteristic grey-green cushions of *Leucobryum glaucum.* Ling (*Calluna*) is killed out by the shade, but when the pinewood has established itself on rather wet heath the pink-flowered cross-leaved heath (*Erica tetralix*) maintains itself better and the purple moor-grass (*Molinia caerulea*) may persist as a low tufted growth. The large fungi are abundant at the time of the autumn rains, especially *Amanita rubescens, Paxillus involutus,* and species of *Boletus* and *Lactarius.*

These southern pinewoods seem to hold their ground indefinitely unless they are destroyed by felling or burning, but it is otherwise with the birchwoods, which also spring up freely on the southern heaths (Phots. 56, 57). Since the birches cast the lightest shade of all our trees, it is only when they have colonised the ground very thickly indeed that they suppress the heath vegetation, which, in a loosely developing birchwood, persists between the young trees, though the heath plants are "drawn up" towards the light. Pine, oak, and beech may sow themselves in the intervals in numbers corresponding with the proximity of adequate seed parents. If the pines are in a great majority they will overtake and kill out the birches and establish a pinewood, but if not, a mixed wood will be formed, in which eventually, on account of their greater height-growth as well as because of the deeper shade they cast, oak will suppress birch and beech will suppress oak (see p. 115).

Thus all four of these trees may be found together on many of our southern heaths (Phots. 81, 82, p. 175) where the sandy soil is sufficiently good and the southern climate favourable to a variety of luxuriant tree-growth.

In the course of the natural succession human interference constantly takes place locally—cutting, felling, burning, planting, or grazing. The result is a patchwork

or mixture of vegetation belonging to the different natural phases, modified by the various types of interference, giving the characteristic landscape of our southern "waste-lands" on sandy soil. This has been called "oak-birch heath," because it is the widespread birches and oaks that are the most constant trees in the succession. Where there are extensive neighbouring pinewoods and beech-woods, these trees also play their part, the pines often comparable in numbers with the birches, and the beeches with the oaks.

SCRUB VEGETATION

Vegetation dominated by shrubs, commonly called "scrub," is in more than one respect intermediate between grassland (or heath) and high forest. What do we mean by a shrub? In the first place, shrubs are of lower stature than trees and they often produce several shoots from the base, a tendency much accentuated by coppicing. Some shrubs, however, for example hawthorn when let alone, form a single trunk which may be as much as 25 feet high, and are then really small trees. On the other hand, many trees (e.g. birch and ash) if cut to the ground in the sapling stage form good coppice shoots, and if the coppicing is repeated remain in the status of shrubs. Thus there is no sharp distinction between shrubs and trees, and in practice woody plants not more than about 20 feet in height at maturity are generally called shrubs. Many kinds, of course, never grow nearly so tall. Dwarf shrubs such as the heaths which do not normally exceed 2 or 3 feet in height are often called "undershrubs." These compete with herbaceous plants on equal terms, so to speak, because they are of comparable stature, and hence must be reckoned as belonging to the "field layer." Most of the heaths and their allies belong to this class, and are not included here with "shrubs" as dominating scrub vegetation.

Secondly, scrub vegetation occupies a position intermediate between herbaceous and tree vegetation both in space and time. Shrubs not only form a distinct layer, between the field and tree layers, in forest vegetation, they also often form a belt between forest and grassland, both on the edges of continental grassland regions and between

subalpine forest and alpine grassland on the higher mountain ranges of the world. In these positions they represent scrub climaxes which are adjusted to climatic conditions intermediate between those of forest and grassland. In succession shrubs commonly precede trees in the seres leading to forest climaxes (see pp. 61, 95-6, 110-15). This is because they reach maturity more quickly, and also because they give useful protection for the germination and establishment of tree seedlings.

Scrub climaxes are represented in the British Islands in positions where wind checks the free growth of trees and prevents them from reaching their proper stature. A good example is the hazel scrub of the Burren limestone region of County Clare in western Ireland (Phots. 58, 59). In a dry climate the limestone would support only a xerophilous vegetation, but in this wet Atlantic coastal climate with its strong moisture-bearing winds and heavy rains there are two main lines of succession. The extensive terraces of largely bare limestone near the sea are colonised by lithophilous (rock-loving) lichens and mosses which in places cover the surface with a thin layer of black humus. In this humus calcicolous plants like the grasses *Sesleria caerulea* and *Koeleria cristata* and the indifferent sheep's fescue, with a number of other calcicolous species, locally form a turf under grazing; but the humus is also colonised by heath plants, since in the wet climate acidity quickly develops in the humus. The ling (*Calluna*) and its associates form mats among the turf on as little as two inches of humus above the limestone rock, and we thus have that curious mixture of calcicoles and calcifuges found also on the English chalk and limestones (see pp. 157, 160).

On the windswept Burren hills extensive areas are dominated by *Calluna* mixed with both calcicole and calcifuge species, but in the rock fissures a number of woody plants also settle down, including hazel, hawthorn, spindle, ivy, blackthorn, and the burnet rose (*Rosa spinosissima*). In much fissured areas these shrubs tend to displace the heath community developed in the humus on the flat limestone surfaces by a scrub, and in the most protected situations continuous and extensive scrub dominated by hazel is actually formed (Phots. 58, 59). The wind, and

to some extent grazing, is the limiting factor, as can be seen on the edge of protected hazel scrub where the violent winds have free access. Here the tops of the hazel shoots are killed back and *Calluna* is successfully competing with the scrub. The same thing is seen where sheep-grazing is fairly heavy and the hazel is eaten back so that it cannot grow more than a foot or two high.

The thick hazel scrub, which in one area, protected by a higher terrace, had a uniform height of about 10 feet (Phot. 59), no doubt corresponding to the level at which its shoots just escape the violent wind, contained hawthorn, blackthorn, and guelder rose, with field rose and bramble, ivy and honeysuckle. Occasional small trees of mountain ash (rowan), one of our most wind-resistant trees, rose a little above the hazel canopy. One of these is shown in Photograph 59. The field layer was well developed, though not rich in species, consisting almost entirely of true woodland (shade) plants, and there was also a moss layer. In less windswept situations in the interior of County Clare there is also a good deal of hazel scrub in the limestone valleys, but here trees, especially ash and on the deeper soils oak, are associated with the shrubs, and the scrub may be regarded as a stage in the succession to climax woodland.

Scrub communities in the midlands and south of England occur in two forms, which have been called *thicket scrub* and *woodland scrub*. Thicket scrub typically forms dense impenetrable growths and largely consists of thorny shrubs such as hawthorn, blackthorn, and gorse, often with bramble and rose, and sometimes with unarmed shrubs interspersed. So dense is the shade cast, especially by the evergreen gorse scrub, that little or nothing can grow beneath it and the scrub is a "one-layered community." Such scrub generally originates on lightly and unevenly grazed grassland where the thorny shrubs are able to establish themselves and increase to a certain extent. Once established they are adequately protected against browsing animals, and patches of thicket scrub come to alternate with pastured grassland.

Arable land on heavy soils too expensive to cultivate when prices are low and which has consequently become derelict, and also abandoned pasture on similar soils, is

R. J. Lythgoe

PHOT. 58. Terraced Limestone Pavement on the Burren, Co. Clare. Dense hazel scrub in the more shelted stretches.

A. G. T.

PHOT. 59. Closer view of hazel scrub in Phot. 58, protected by higher terrace on the left. The emerging tree is mountain ash, very resistant to wind. The man standing on the floor of the wood indicates its height.

often covered with thicket scrub overwhelmingly dominated by hawthorn, as can readily be seen in many parts of the country. Examples have been studied in south-west Cambridgeshire on chalky boulder-clay. The scrub develops rather slowly and unevenly on abandoned pasture, more rapidly on abandoned arable land, giving a denser and more even-aged scrub. Dog-rose (*Rosa canina*) and one of the sweet briars (*Rosa micrantha*) colonise the ground along with the two hawthorns (*Crataegus monogyna* and *C. oxyacanthoides*), and a few other woody species are present, including the small-leaved elm (*Ulmus minor*) which suckers from neighbouring hedges and grows taller than the hawthorns. This elm, in fact, is the only species of tree which may locally suppress the hawthorns in this region, forming small patches of woodland. Seedlings and saplings of ash and oak, which are the dominant species of the infrequent semi-natural woods of the region, are no more than rare or occasional and show no ability to form woodland.

The two factors which determine the course taken by this subsere are the attacks of rabbits and the great quantity of hawthorn seed available, contrasting with the paucity of seed parents of the other woody plants, such as ash and oak. Rabbits are common and in some places very numerous, so that they bark and sometimes kill the hawthorns and elms as well as eating down the herbage. They destroy the seedlings of unarmed trees and shrubs unless these are well protected by the hawthorns.

As the hawthorn scrub grows up and closes in, the other woody plants are suppressed, only a few bushes remaining in gaps. The oldest hawthorn scrub examined was more than 50, probably over 60, years old and about 18 feet high, with completely closed canopy casting very deep shade. The ground was almost entirely bare of vegetation, covered with a litter of dead leaves and twigs. The field layer was extremely sparse, indeed almost non-existent, including only 5 species and only 2 true woodland plants—dog's mercury and stinging nettle. The few mosses were mostly growing on fallen and rotting branches. This old scrub appeared to be senescent, so that the span of life of the hawthorn scrub here is probably less than a century. Its development forms a good example of deflected succession.

Scrub Vegetation

Woodland scrub comprises the seral communities dominated by shrubs during the process of development of woodland, tree saplings being abundant among the bushes. Examples of the woodland scrub belonging to different seres have been given when we were describing the development of the various types of woodland (pp. 96, 110-15). Woodland scrub is generally loose as compared with thicket scrub, because the trees begin to acquire dominance and check the multiplication of shrubs before the latter have formed a closed community. When a factor like grazing or rabbit attack intervenes, not heavy enough to prevent the development of woody plants altogether, but sufficient to check the progress to woodland by destroying most of the tree seedlings and saplings and damaging the shrubs, particularly the unarmed shrubs, woodland scrub tends to be converted into thicket scrub mainly composed of thorny species, because it is these that are most able to maintain themselves and even to multiply in the face of animal attack.

The field layer of dense thicket scrub is, as we have seen, practically absent. Round its edges, where the clumps of scrub abut on grassland, there is often a narrow belt of "marginal" or "half-shade" species, since in this position they are partly shaded and to some extent protected, because grazing animals, except rabbits, do not graze right up to the bushes.

The field layer of woodland scrub is extremely mixed. First there are surviving species of grassland plants when the woodland subsere starts on abandoned pasture, or of arable weeds when it starts on abandoned ploughland. Then there are the marginal or half-shade species, which form the most characteristic element of the field layer of woodland scrub just as they are of coppice, of hedgebanks, and of the edges of established wood or thicket. Finally there are the forerunners of true woodland or shade plants.

The marginal or half-shade species are a considerable proportion of the British flora, but they do not form a sharply defined class, because a great number of them are able to flourish in full illumination and may occur in grassland which is not heavily grazed, where they find some protection and not too much competition, while others may

exist, at least for a time, though they may not flower, in deeper shade. The requirements of every species depends on its individual constitution, and correspondingly the *range* of each, in respect of each of the different factors of the habitat, is different. Within the extreme range through which a species can *exist* there is a narrower range of relatively optimum conditions in which it can *flourish*, and a habitat which commonly affords these optimum conditions for a number of species is inhabited mainly by a biological class, such for example as the marginal or half-shade plants. But the class is not sharply defined, because both the extreme range and the optimum range of many of the species may extend beyond the range of conditions commonly realised in the habitat.

Besides woodland scrub, where partial shade is the prevalent condition, and the edges of woodland and of thicket scrub, the hedgerows which are almost universal in the south and midlands offer closely similar habitats. A hedgerow is a line of artificial scrub and is itself often colonised by shrubs and trees which spring up between the planted shrubs. Alongside the hedge, and on the hedgebank, partial shade is found, and this is a favourite habitat of many of the marginal or wood-edge species. Coppice is another. We saw (p. 68) that regular coppicing impresses a periodicity on the field layer of a wood corresponding with the change from full illumination immediately after the coppice is cut to deep shade when it is fully grown. During much of the period, however, the conditions are those of partial shade, and along with the true woodland species a number of marginal plants occur in coppice.

The following is a small selection of a dozen common and characteristic "marginal" species: wild basil (*Clinopodium vulgare*), teasel (*Dipsacus silvestris*), common willowherb (*Epilobium montanum*), crosswort (*Galium cruciata*), *G. mollugo*, hairy and perforate St. Johnsworts (*Hypericum hirsutum* and *H. perforatum*), red campion (*Melandrium dioicum*), creeping tormentil (*Potentilla procumbens*), orpine (*Sedum telephium*), stitchwort (*Stellaria holostea*), germander speedwell (*Veronica chamaedrys*), ground ivy (*Nepeta hederacea*).

CHAPTER IX

THE GRASSLANDS

Meadow, Pasture, and Chalk Down

We have seen in earlier chapters that grassland of one sort and another occupies the greater part of England and Wales, as well as very much of Ireland and a considerable portion of Scotland, though the "natural" vegetation of most of the area now occupied by grass is deciduous forest. The origin and continuous maintenance of this grassland within the climatic limits of forest are due entirely to grazing animals. In the absence of these forest would reoccupy the country; but the fact that it is plant communities dominated by grasses rather than by other kinds of plants which replace forest when any area is pastured, depends upon the structure and life economy of the grass plants themselves and upon a climate that favours them.

The *turf-forming* type of grass, the characteristic grazing type of which our meadows and pastures are predominantly formed, produces numerous lateral shoots ("tillers") from the base or stock of the plant which is embedded in the surface of the soil. If left alone these tillers produce leaves and eventually erect flowering shoots, but if the erect shoots are constantly removed by grazing or mowing fresh shoots are as constantly formed from the base. The new shoots grow out laterally close to the soil surface, and it is the feltwork of these, together with the mass of fibrous grass roots densely filling the upper two or three inches of soil, that forms the turf or "sole" of a closely grazed pasture or well-tended lawn.

What is often called the *meadow* type of grass consists of taller-growing grasses traditionally cut for hay and not forming so close a turf as the pasture type, partly because of their freer habit but mainly because their upward-growing shoots are not constantly removed during their growing season as when they are grazed. There is no sharp distinction between the two types and many species of

grass flourish equally well in pasture and hayfield, the habit being more or less modified by the treatment.

Differing from the pasture and meadow types are the *tussock-forming* grasses whose vegetative parts are coarser and harder, so that the dead bases of the leaves and stems decay with difficulty, accumulating humus between them. Thus a "tussock" is formed, which persists and gradually increases in size, projecting several inches above the soil. The *stooled* type is an exaggerated form of the tussock type. Such grasses increase in badly tended and especially in wet meadows and are unsuitable for grazing, and usually also for hay.

Since the majority of the grasses are shallow-rooting plants, they depend for good growth on a more or less constant supply of water in the surface layer of soil, and this they can only get (apart from irrigation) from frequent rains during their principal growing season, April to June. Continuous dry weather during these months leads to a poor hay crop and deficient summer pasture. If there is prolonged drought in late summer the grasslands turn brown and are only revived by the wet weather usual in autumn. The frequent though not heavy rains of a "normal" season in Britain are therefore peculiarly favourable to the continued growth of grass, and when there is a mild "open" winter this growth continues practically throughout the year. It is the more abundant rainfall and moister air of the north and west, and of Ireland, that has made these parts of the country the great natural grazing areas, while the east and south, drier and with warmer summers, are the best for arable crops.

Though growth may continue slowly throughout the winter whenever the temperature is not too low, the most active growth of the grasses, as of course of most plants in our climate, is in the spring when the temperature begins to rise. It is then that the meadows become more vividly green and the fresh sappy growth yields the most palatable and nutritious food for stock. About midsummer, when most of the grasses flower if they have not been eaten down, vegetative growth slackens. In meadows which have been allowed to grow up for hay, growth is resumed after the hay crop is cut at midsummer, quite actively if there is

enough rain in July and August, and this "aftermath" affords good grazing into the autumn.

The constant removal of the vegetative shoots of the grasses, by grazing animals or by mowing, while it immediately stimulates fresh vegetative growth, also leads to the need for replacement of nutritive elements contained in the young shoots that have been lost, and this has to be supplied from the soil. The dung of the grazing stock returns a certain quantity of plant food to the ground, but unless the animals are largely fed away from the pasture there will clearly be a debit balance to the soil represented by the increase in weight of the pastured stock. To meet this and keep a pasture "in good heart," dung from other sources is spread on the ground by hand. Dung, however, is deficient in certain elements, such as lime and phosphates, which are needed by the soil and by plants, and artificial manures such as lime or powdered chalk and superphosphate or basic slag are used as a supplement to the dung. Apart from the supply of calcium to the plants, the lime or chalk has good effects on the soil itself (see p. 81), and it is this which is the real function of "liming." Though calcium is essential to the nutrition of plants, it is not needed in such quantity for this purpose, and there is nearly always a sufficient reserve in the soil minerals. Soils deficient in potash can be manured with kainit. The all-important nitrogen too, though there is plenty of it in farm-yard manure, can be supplied in a more immediately available form as a nitrate or as sulphate of ammonia.

To keep a pasture or hayfield or lawn in good stable condition an equilibrium must be established between the removal of plant substance through grazing or mowing and the supply of essential chemical elements in dung or artificial manures. If this is not done the grassland "runs down," the soil gradually loses its fertility, the best grasses and other good pasture plants are replaced by species which make less demand on the soil, i.e. by "weeds," and the pasture eventually becomes valueless. While this is happening the land, of course, will carry less and less stock. Consequently it is "undergrazed," the spring shoots are not eaten off but remain into the summer, when they become unpalatable and innutritious, and the pasture is often

invaded by woody plants and tends to "revert" to scrub. Thus a vicious circle is established, and the only way to break it is to plough up the pasture and replace the grass by a succession of arable crops properly manured so as to restore fertility. The general aspects of this problem are considered in Chapter XVIII.

Most of the British grassland and nearly all of that in the English lowlands is, as we saw in Chapter I, in the form of "permanent pasture," and though a good deal of this has been ploughed up during the war much of it still remains. Permanent pasture is what is called a "semi-natural" type of plant community, for though it may have been originally sown on formerly arable land it behaves like a natural plant community subject to the effect of continuous grazing.

Permanent grassland of this type is occupied by pasture and meadow-grasses of the type described on p. 186. These are for the most part exacting plants flourishing only on a "good" soil rich in nutritive salts. Most of them have slender "stocks" and grow by "tillering," for example perennial rye-grass, cocksfoot, timothy, crested dog's-tail, etc. Tussock-forming grasses (p. 187)—such, for instance, as the tufted hair-grass (*Deschampsia caespitosa*)—are not for the most part palatable to stock, and must be regarded as "weeds" in pasture. A pasture infested with them becomes of little value. The leaves of most pasture and meadow-grasses are relatively broad and soft, contrasting with the narrow or bristle-shaped leaves of the grasses which inhabit most of the hillside rough grazings. They are vividly green in April and May, their most active period of growth; and when the season is wet, continuously into the autumn so long as the weather is not too cold. In long summer droughts the pastures turn brown.

Collectively the communities dominated by meadow-grasses may be called *neutral grassland*, because they contrast with the two types of rough grazings—with those developed on the chalk and other basic soils on the one hand and with those occurring on the acid soils of the siliceous hills on the other. In general, also, the soil reaction of these grasslands is in the neighbourhood of the neutral point though often somewhat acid; and some of

the alluvial meadow soils are actually as alkaline as typical chalk or limestone pastures. The soil reaction (*p*H value) is not in fact the decisive feature of the habitat of the meadow-grasses, which require for their permanent well-being a well-aerated soil with abundance of nutritive salts, moderate continuous moisture, and properly regulated grazing.

While most of the neutral grassland is enclosed in fields which have been at one time ploughed, there is a certain amount on the edges of old woods, on the grass verges of roadsides, and on commons and village greens, which has never been ploughed or sown, but was at one time forest land, converted into grassland by felling and grazing alone. This is the most "natural" kind of neutral grassland, because it is never tended and is maintained as grassland solely by grazing or cutting; if ungrazed it is quickly invaded by shrubs, and in the neighbourhood of woodland by trees.

The communities of neutral grassland are very varied. Commonly several grass species are co-dominant and mixed with a variety of herbs. Sometimes a particular grass becomes dominant over a certain limited area. It is important to recognise that the actual nature and composition of a particular area depends (subject to general conditions of soil and water supply) almost entirely on its treatment. Differential manuring or different grazing regimes will produce widely different grassland communities, and the kinds and degrees of cultivation (or neglect) are almost infinitely various. Thus a grass field may be intensively grazed, or it may be undergrazed, by sheep, by cattle, by horses, or by mixed stock, at various times of the year. It may be manured with dung, or with various artificial manures in any proportions; it may be harrowed or rolled; it may be "put up" for hay at intervals. Every combination of these factors will produce a somewhat different, often a widely or almost totally different, flora.

The profound effects of manuring with different "fertilisers" was demonstrated more than half a century ago in the classical experiments on the park grassland at Rothamsted. Here a uniform stretch of old pasture on heavy loam was divided into separate plots, each of which received a different manurial treatment which was consistently maintained for many years. The herbage was cut once in each

year and the percentage composition of the vegetation of each plot separately determined. A number of different "new" species (24 in all) appeared in the various plots which received particular fertilisers, and some of them came to dominate the vegetation so that the appearance of the plots in the early summer was widely different. The largest number of species (61) on any plot occurred on the unmanured plots, but none was dominant, and only 2—sheep's fescue and common bent—formed more than 10 per cent. of the herbage. These two grasses are the dominants of the untended acidic pastures of the siliceous hillsides of the north and west which are dealt with in the next chapter. While they were present in some of the manured plots they were never prominent in them. They are essentially tolerant of poor soil and are unable to compete effectively with the more luxuriant grasses and herbs of manured grassland. Sheep's fescue is typically absent from the meadow-grass communities, and common bent is prominent only in those on the poorer soils.

The great variety of species on the unmanured plots included many which are of no value in pasture because they are unpalatable or innutritious to stock. High manuring tends to exclude these because it favours on the whole particular exacting species which are the best pasture plants. Among the latter perennial rye-grass (*Lolium perenne*) and white clover (*Trifolium repens*) are pre-eminent, and the best pastures are largely dominated by these two plants. The vigour of these two species on really good soil tends to exclude other plants and thus to reduce the total flora. Both are also resistant to trampling, so that they often grow in the foot tracks across meadows, or (when the centre of the track is worn bare) on the sides of the path where the traffic is not so constant. Perennial rye-grass is much commoner in rich, well-tended pastures than in any wild habitat. Its inflorescence is a characteristic spike of flattened alternating spikelets [1] on the two sides of the stalk.

[1] A grass "spikelet" is the close aggregation of a few of the tiny grass flowers, and forms the unit of a grass inflorescence. The spikelets are arranged in very various ways in the inflorescence as a whole. The scales surrounding each spikelet are called "glumes," and these sometimes bear long bristle-like "awns."

Cocksfoot (*Dactylis glomerata*), with its characteristic branching inflorescence made up of separated dense ovoid aggregations of spikelets, is another valuable grass both for hay and pasture, and is abundant on many soils, both in "natural" situations, such as wood-edges and roadside verges, and in well-tended grassland. It is a strongly tufted grass of rather coarse habit, and on rich soil its flowering stems may reach a height of 4 feet.

Meadow foxtail (*Alopecurus pratensis*) grows in large rather loose tufts and is of coarse tall growth, the vegetative shoots 2 feet high, the terminal cylindrical inflorescences attaining a height of 3 feet and developing in May. It flourishes best, and is often dominant, in meadowland regularly cut for hay.

Timothy (*Phleum pratense*) is also a tall tufted grass, as much as 4 feet high, again with compact cylindrical spikes, and flourishing best in hayfields on good, rather heavy soil, usually disappearing under pasture. It develops much later in the season than meadow foxtail.

Crested dog's-tail (*Cynosurus cristatus*) is a shorter grass, and unlike the two preceding species flourishes better in pasture than in permanent hayfields, occurring on a considerable range of soils, both dry and damp. It is a valuable grass in second-class pastures, where it is often dominant or co-dominant, taking the place of the perennial rye-grass of the best pastures. The toothed ("crested") glumes of the compact one-sided inflorescences are characteristic.

Two species of *Poa* ("meadow-grasses" in the narrower sense) are very commonly mixed with other grasses in meadowland. They have characteristic loose elegant inflorescences with very small spikelets. *Poa pratensis* (common meadow-grass, "Kentucky bluegrass" in America, where it was introduced long ago and has spread to much of the prairie land) is the only true meadow-grass with an underground creeping rhizome. It is particularly resistant to treading and is consequently often dominant on or by the side of footpaths across meadows. *Poa trivialis* (rough-stalked meadow-grass) is commoner in wet meadows. It has creeping stolons and is of value as a pasture grass on suitable soils. *Poa annua* is a ubiquitous annual weed, the

commonest grass weed in garden beds and paths, and often dominant for a time on freshly disturbed soil.

Several species of fescue occur in neutral grassland. Meadow fescue (*Festuca pratensis*) is a widely distributed and valuable grass in the lowlands. Tall fescue (*F. elatior*) is coarser and more robust, though well taken by stock. It is said to be more hardy and to do better on poorer and drier soils than meadow fescue, as well as on heavy clays. Red fescue (*Festuca rubra*) has much narrower leaves (in some forms bristle-shaped) than the foregoing species. It has several varieties and some commonly occur in neutral grassland: red fescue is sometimes locally dominant in pasture, where it forms a close well-grazed turf of shortly creeping shoots.

Common bent (*Agrostis tenuis*) is a very widely distributed and abundant grass alike in neutral and acid pastures and on grass heaths. Probably its individuals are more numerous than those of any other British grass with the possible exception of *Poa annua*. In the poorest pastures on a great range of soils, from sandy loam to heavy clays, common bent is often dominant over wide areas, sometimes forming 90 per cent. of the herbage. It also occurs freely in medium pastures on somewhat acid soil, mixed with the better grasses. Here it is of very limited grazing value, maturing late in the season, and its short, rather scabrid leaves soon wither in poor dry pasture, becoming quite useless for stock in late summer. Abundance of common bent is as much an index of the poverty of a neutral pasture as perennial rye-grass is of its richness.

Fiorin or white bent (*Agrostis stolonifera*), of quite extensively creeping habit, is also a widely distributed pasture grass, especially in moister and better soils, and is of distinct agricultural value on wet and heavy ground.

Sweet vernal grass (*Anthoxanthum odoratum*) is another very widely distributed grass on a great variety of soils, though it is never dominant. It is tufted and of very variable size and habit, flowering in late April or early May, before any of the other grasses. It is particularly rich in the substance (*cumarin*) which gives the characteristic smell to new-mown hay, and it tends to be calcifuge.

False oat-grass (*Arrhenatherum elatius*) is a tall, coarse,

strongly growing grass up to 4 feet in height. It persists well under cutting but cannot endure grazing. It frequently colonises and becomes dominant on disturbed soils such as the grass verges of roadsides (particularly on calcareous soil), where it is cut every year, and produces abundant hay though of poor quality. The single long awn projecting from each spikelet, and the large loose spreading inflorescences, long and narrow in fruit (when the branches close up to the central axis), are characteristic.

Two very common grasses which are troublesome weeds in pastures are Yorkshire Fog (*Holcus lanatus*) and tufted hair-grass (*Deschampsia caespitosa*), which has already been mentioned. Yorkshire Fog is a ubiquitous, very aggressive grass on good soils, and since it increases under manuring, it often forms a large proportion of the herbage of good pastures, spreading vegetatively in rosette-like tufts. Its broad leaves are covered with soft hairs and are generally refused by stock. Tufted hair-grass forms large tussocks or stools with very long, narrow, harsh, widely spreading leaves, finely serrated along the margins, and large loose inflorescences with very small spikelets. This grass flourishes especially on soils which tend to be waterlogged.

Average neutral grassland contains, of course, many species of flowering plants besides the grasses. Of these, agriculturists generally distinguish the members of the pea family (*Leguminosae*) because they are useful pasture plants, some as valuable as the best grasses, while many, though not all, of the remaining "miscellaneous" species are practically worthless for stock. Leguminous plants contain on the average more protein, much more calcium, and less carbohydrate than grasses, and are thus highly nutritious. In addition they "fix" free nitrogen from the air, leaving it in the soil in a form available as plant food, and are thus of great importance in enriching the soil. Leguminous plants are practically always present in neutral pasture, though not specially numerous in species and individuals. They are much encouraged by phosphate and potash manures such as basic slag and kainit.

The clovers (*Trifolium*) are the most widely distributed and abundant. Red clover (*T. pratense*) is a free-growing

tufted perennial occurring on many different kinds of soil, more abundant in old meadowland cut for hay and a valuable accumulator of nitrogen. The cultivated varieties are often sown as arable crops (for clover hay). White clover (*T. repens*) propagates very freely by means of runners, especially in pasture, on a wide variety of the better soils. It is one of the most valuable of agricultural plants and is, as we have already seen, characteristically associated with perennial rye-grass in the best pastures, and remarkably resistant to trampling and rolling. That is one reason why it is so common on lawns, and if a new foot track is worn across a grass field or meadow in which white clover is present this will often increase and become dominant on the path because it can withstand the constant pressure of feet better than most of the grasses. Yellow suckling clover (*T. dubium*), a smaller annual plant with much smaller heads of minute yellow flowers, is not nearly so valuable as these two, because of its lesser bulk, but it is widely distributed and of some use in pasture. Black medick (*Medicago lupulina*) is also a small annual, very common, and with a strong superficial resemblance to suckling clover.

One of the most widely distributed leguminous plants is the handsome yellow or orange-flowered bird's-foot trefoil (*Lotus corniculatus*), which occurs on a much wider variety of soils than do the clovers, not only on neutral grassland but also in chalk and limestone pastures, on grass heaths and in bent-fescue hill grazings. This plant has a long root so that it can tap water supplies when the surface soil dries out, and is no doubt of considerable value in pasture though never treated as an agricultural plant. The yellow-flowered scrambling meadow vetchling (*Lathyrus pratensis*) is another common leguminous plant of neutral grassland, particularly in hayfields and by roadsides, and so are more than one species of crimson or pink-flowered vetch of similar habit, such as the common "tare" (*Vicia sativa*), which is sometimes sown as a crop, and the narrow-leaved vetch (*Vicia angustifolia*).

"Miscellaneous" plants, i.e. species which are neither grasses nor leguminous, are so numerous that it would take too much space to attempt to deal with any wide selection,

but a few of the commonest and most noteworthy may be mentioned.

Three kinds of buttercups are very common: bulbous buttercup (*Ranunculus bulbosus*), flowering in late April and May, whose golden flowers have strongly reflexed sepals; field buttercup (*Ranunculus acer*), a taller, rather later flowering plant; and creeping buttercup (*Ranunculus repens*), propagating itself freely by runners which readily root, very common on heavy soils, where it is a persistent garden weed. All are useless for stock, and even mildly poisonous.

Milfoil or yarrow (*Achillea millefolium*), with its leaves cut into narrow filiform segments, and conspicuous flat-topped white or pink inflorescences appearing in late summer and early autumn, is abundant in many kinds of neutral grassland. It is a deep-rooted, drought-resistant plant, its foliage remaining fresh and green at the end of a hot dry summer when most of the herbage is dried up. It is often well cropped by stock and is thus of considerable value in pasture. When growing gregariously it forms a dense "sole" in the turf, excluding other plants. Another species, sneezewort (*Achillea ptarmica*), is less common, but may be abundant on rather wet heavy soil.

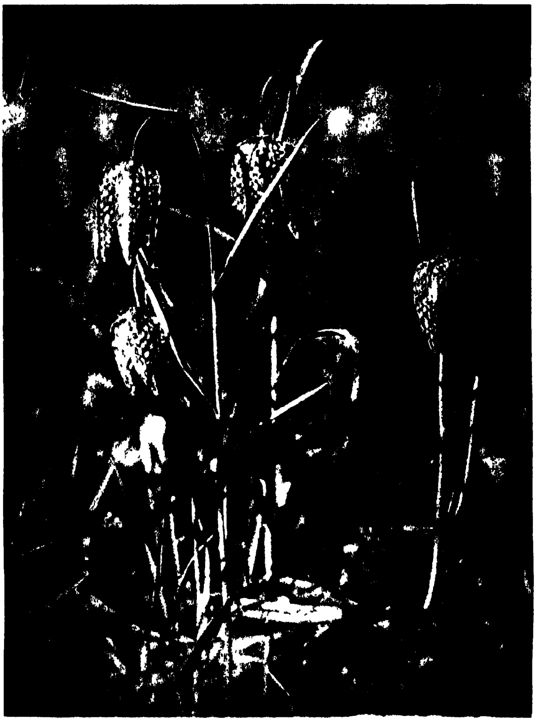
Ribwort plantain (*Plantago lanceolata*) is a very abundant plant on all kinds of soil except acid peat. Like milfoil, it is deep-rooting and drought-resistant and certainly has a value in many pastures, though it is useless for hay because the leaves are not easily caught by the machine and even if harvested are difficult to dry. Ribwort may, however, increase so much at the expense of better pasture plants as to become a troublesome weed. Its pollen causes hay fever.

The beautiful meadow cranesbill (*Geranium pratense*) with its large, blue, widely open flowers, is a much more "local" plant of neutral grassland, but is usually abundant where it occurs. Various other small red-flowered species of cranesbill (wild geranium) are often found.

Yellow rattle (*Rhinanthus crista-galli*), so called from the rattling noise of its ripe detached seed in the pods when these are shaken by the wind, is a weed whose roots are parasitic on the roots of grasses. It is said to be an infallible index of poor grassland on heavy soils, where it

The Times

PHOT. 60. Wild daffodils in clay pasture, Dorset.



N. F. G. Cruttwell

PHOT. 61. Snake's-head fritillary, Magdalen Meadow, Oxford. May.

The Times

PHOT. 62. The South Downs from the Devil's Dyke (extreme left) to Chanctonbury Ring (a clump of planted trees on the summit) in the distance—8 or 9 miles. Below the ring the escarpment is covered with beechwood, but the rest of the stretch is typical chalk grassland with a very little scrub. The village of Poynings is in the centre foreground. The edge of the Weald is covered with arable fields.

sometimes becomes almost dominant. Of other coarse pestilent weeds of neutral grassland the docks (*Rumex*) and thistles (*Cirsium*) are the worst. They produce abundant very easily distributed seed, and in grassland which is entirely neglected may become dominant.

Finally three bulbous plants of neutral grassland, with conspicuous flowers, may be mentioned, all of which are decidedly "local" in distribution, but all gregarious and all highly decorative. These are the daffodil (*Narcissus pseudo-narcissus*) (Phot. 60), which in April turns some meadow-lands golden, especially in the west of England; meadow saffron (*Colchicum autumnale*), growing also in woods and along wood-edges, leafing in spring and producing its crocus-like pale crimson flowers in autumn, long after the leaves have died down; and the extremely local snake's-head fritillary (*Fritillaria meleagris*) (Phot. 61), with its elegant, drooping, bell-shaped flower, dusky purple and spotted, or pure white, which grows in alluvial meadows.

Very wet grasslands where the surface soil is waterlogged for a great part of the year support grasses and other plants which are tolerant of such conditions, together with the species which flourish only where the soil is constantly wet. These include, of course, genuine marsh plants. A very common community constantly seen in permanent pasture on heavy clay is dominated by species of rush (*Juncus*) with their slender cylindrical dark green stems and leaves, springing from a stout underground rhizome. Between the tufts of the rushes grow wet-loving grasses and various marsh plants, including more species of sedge (*Carex*) than are found in the drier meadows.

Water meadows are alluvial meadows which are regularly irrigated from the stream or river beside which they lie. Under natural conditions they are irrigated by periodic flooding, mainly in winter when the river water rises after heavy rains in its drainage basin; and these floods bring a deposit of fertilising silt to the meadows. By embankment and the construction of sluices and irrigation channels the flooding is regulated and the water meadows brought into a systematic regime. The regular water supply, the abundant mineral elements contained in the silt, and the good aeration resulting from the dissolved air brought by the

moving water lead to luxuriant growth of the vegetation, which was generally cut for hay.

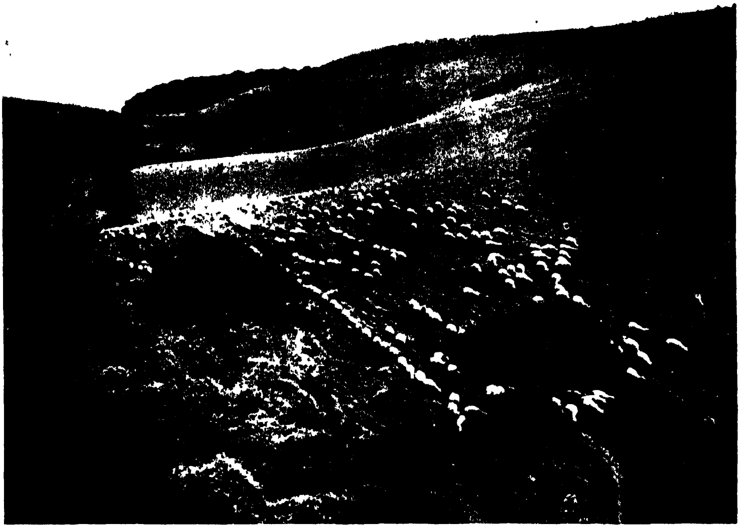
A considerable variety of grasses and other herbs flourish under these conditions, not only water-loving grasses, such as *Glyceria maxima* (*aquatica*) and *Phalaris arundinacea*, but for the most part grasses abundant in ordinary meadows. The bulk of water-meadow hay is actually composed of ordinary meadow-grasses. Among the herbs other than grasses there are a considerable number of marsh plants, but also many species which tolerate both very wet and less wet conditions.

Many of our water-meadow systems are now in decay, the sluices and channels neglected and largely derelict; and most alluvial meadows are used as pasture.

CHALK AND LIMESTONE GRASSLAND

The grassland of the chalk downs of southern England is one of the best characterised and also one of the most attractive of our semi-natural grassland communities. The downs of Kent, Sussex, Hampshire, Dorset, Wiltshire (including Salisbury Plain), and Berkshire, and smaller areas in Surrey, Buckinghamshire, Oxfordshire, Bedfordshire, and Hertfordshire, are largely covered with this special type of pasture, recognisable almost at a glance, which forms by far the largest area of "rough grazing" in the south of England. Chalk pasture proper does not, however, extend over the whole outcrop of the chalk, but is for the most part limited to the slopes of the escarpments and valley-sides and the summits of the narrower ridges. The greater part of the chalk outcrop is undulating plateau land, and here the chalk rock itself is nearly everywhere covered by a deposit of clay or loam of varying thickness which is occupied mainly by arable land. It is chiefly on the steeper slopes where the soil is very thin over the chalk—too shallow for the plough—and consequently highly calcareous, that it is left in grass vegetation, and this is "downland" proper. Photograph 62 shows a typical stretch of the escarpment grassland of the South Downs.

Chalk pasture is traditional sheep pasture and has probably been so continuously from Neolithic times, though

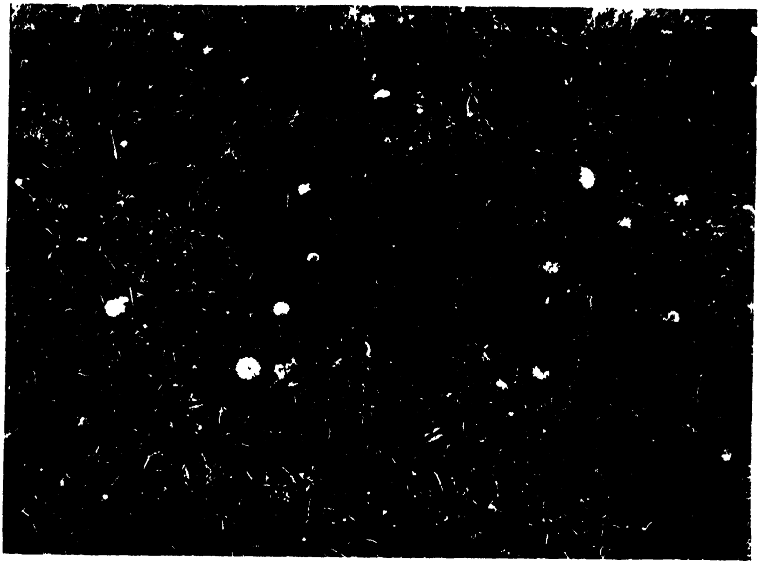


The Times

PHOT. 63. A large flock of sheep returning from pasture on the downs, mostly keeping to the parallel tracks they have made along the face of the escarpment. Mount Harry near Lewes.

The Times

PHOT. 64. Chalk escarpment of the Chilterns. Grassland with wind-cut juniper scrub. A group of elders occupies the rabbit burrows in the centre. At the foot of the escarpment is a terrace of fertile arable land (Upper Greensand) with light-coloured fields, and the plain of Aylesbury beyond.



A. G. T.

PHOT. 65. Sheep-grazed chalk grassland of sheep's fescue and glaucous sedge. Ladies' bedstraw in the centre, and pappus fruits of hairy hawkbit are conspicuous, with heads of the small scabious (right and left centre).

A. G. T.

PHOT. 66. Chalk grassland heavily eaten down by rabbits. The long narrow leaves of the glaucous sedge, the basal leaves of a thistle (bottom right) and the dominant mosses, which are luxuriant here because the area is shaded by a wood, are all avoided by rabbits. Most other plants are suppressed.

in recent years the great flocks of sheep which once fed upon it have been very much reduced and partly replaced by cattle. Photograph 63 shows a flock of sheep descending from South Down pasture along the parallel sheep tracks they have created, and Photograph 64 a typical view on the Chiltern escarpment with scattered juniper scrub. A great deal of chalk grassland—far too much—is, however, very heavily infested by rabbits, which eat down the turf so close to the soil as to make it quite useless for sheep or cattle. Full sheep-grazing reduces the herbage to two inches or under, but rabbits in great numbers may reduce it to half an inch. Down turf which is moderately grazed by rabbits, with herbage about an inch high and very compact owing to the great production of interlacing lateral shoots, forms the velvety but springy carpet that is so delightful to the walker on the downs. This is partly due to the crispness and elasticity of the plant shoots, particularly of the fine-leaved fescues, which compose it, and partly to the dryness of the soil beneath. Photograph 65 shows the vegetation of a chalk down grazed by sheep and with an abundance of flowering plants. Photographs 66 and 67 are of heavily rabbit-grazed areas, while Photograph 68 is of an area adjacent to that shown in 67, but fenced against all grazing for 6 years.

The dominant grass of well-grazed down pasture is sheep's fescue (*Festuca ovina*), and with this is associated red fescue (*Festuca rubra*) in almost equal quantity. These two grasses are superficially very similar—rather small tufted plants with long bristle-like leaves—but the red fescue forms lateral shoots which escape from the sheath of scales at the base of the tuft and creep on the soil, though only for a short distance. Neither is in any way confined to chalk grassland: on the contrary they are common on all kinds of dry and poor soils, and sheep's fescue is co-dominant with common bent (*Agrostis tenuis*) on the very extensive siliceous pastures of the western and northern hills; but nowhere is it so overwhelmingly dominant alone, or together with red fescue, as on the chalk and limestone, where these two species often form much the largest bulk of the herbage. In the driest situations sheep's fescue is usually dominant alone.

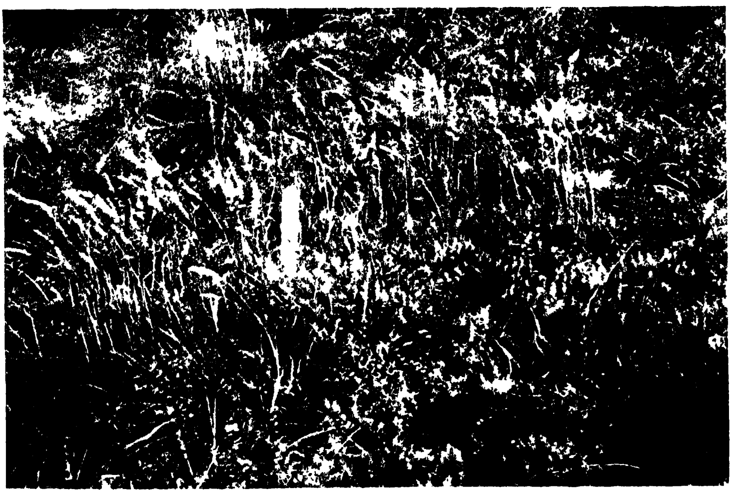
A number of other grasses are both characteristic and abundant on the chalk. Some of them are taller plants than the fine-leaved fescues, and when grazing is not so heavy they may grow up and become dominant. Prominent among them are the oat-grasses with long awns projecting from the spikelets. The commonest is common oat-grass (*Avena pratensis*) with two awns on the spikelet. This is sometimes replaced by the downy oat-grass (*Avena pubescens*). Golden oat-grass (*Trisetum flavescens*) has an attractive yellow colour and three awns on the spikelet. Any of these may become locally dominant. False oat-grass (*Arrhenatherum elatius*, see p. 148), with one awn on each spikelet, also occurs and may become dominant on disturbed chalky soil, but it is intolerant of grazing and not characteristic of chalk pasture. A common habitat is waste land and roadside verges, especially on calcareous soil, which are cut but not grazed, and here it is often dominant along great stretches.

A fairly tall grass which is dominant on some downs is upright brome (*Bromus erectus*) with compact ovoid spikelets which have a silvery sheen as they pass into the fruiting stage. This is rather intolerant of grazing, at any rate heavy grazing, but can colonise dry bare chalk soil just as sheep's fescue can. In southern England it is found mainly on chalk and oolitic limestone, but it is rather local, though commonly dominant where it occurs in quantity.

Tor-grass (*Brachypodium pinnatum*) is often closely associated with the brome, but on many downs it appears almost exclusively in nearly pure, actively spreading circular patches which catch the eye at once by their light-yellowish colour. It has spread widely and increased substantially in abundance during the last half-century, but is still confined to the south and east of England and is far commoner on the chalk than on other soils. The spread of tor-grass seems to be connected with the fall in the number of sheep grazing the downs. Its leaves are eaten by them in the young condition, but when the plant is once allowed to mature the foliage becomes rather dry and innutritious and is refused by both stock and rabbits, so that there is nothing to interfere with the spread of the grass, which thus ruins the land for pasture.

A. G. T.

PHOT. 67. Uneven ground fully exposed to rabbits. Herbage barely 3 inches deep. Rock-rose (in flower) and thistles, both avoided by rabbits, are conspicuous.



A. G. T.

PHOT. 68. Area near Phot. 67. Rabbits excluded for 6 years. Herbage at least 8 inches deep. Yorkshire Fog (centre and left) and ladies' bedstraw (in front and right) are dominant. Both would have been eaten down if rabbits had had access.

Shorter grasses, which do not become dominant but are very frequent in and characteristic of chalk pasture though by no means confined to it, are *Koeleria cristata*, sometimes called "crested hair-grass," and quaking-grass (*Briza media*), with widely separated dense ovoid spikelets trembling in the wind on their long slender flexuous stalks. Quaking-grass is characteristic of land which is very poor and dry, and it sometimes also occurs on poor wet soils. Unlike *Koeleria*, it is worthless for stock.

All these ten species of grass may be called "characteristic" of chalk grassland, because of their constant occurrence in the community, though several are more or less commonly found in other kinds of grassland. Only the oat-grasses and *Koeleria* are decidedly commoner on the chalk than on any non-calcareous soil, while tor-grass and upright brome are practically confined to chalk and oolite.

Of other grasses, in no sense characteristic of chalk, cocksfoot (*Dactylis*) occurs in three out of four samples and so does sweet vernal grass (*Anthoxanthum*). Crested dog's-tail (*Cynosurus*), timothy (*Phleum pratense*), and common meadow-grass (*Poa pratensis*) are decidedly less common, occurring in about one sample area out of three. The exceedingly widespread and abundant common bent (*Agrostis tenuis*) is very exceptional in chalk pasture, and all the grasses that favour acid soils are of course quite absent. Fiorin (*Agrostis stolonifera*), on the other hand, occurs pretty frequently; Yorkshire Fog (*Holcus lanatus*), that aggressive weed of many pastures, occurred in about half of a great number of areas examined: it often spreads rapidly when heavy rabbit pressure is withdrawn (Phot. 68).

Tall meadow-grasses not at all characteristic of chalk, such as tufted hair-grass (*Deschampsia caespitosa*) and tall fescue (*Festuca elatior*), which require abundant moisture, may flourish on temporarily ungrazed, cool, steep, north-facing slopes, where the shallow soil, though still highly calcareous, is black with excessive humus and always more or less damp; and their luxuriant growth then suppresses most of the lower-growing chalk plants, thus completely altering the vegetation.

The characteristic herbs of chalk grassland other than grasses are numerous, and many have bright attractive

flowers. As with the grasses, some of them are characteristic because of their constancy or abundance in this community and others because they are rarely or never found anywhere else.

The little sedge *Carex flacca* (Phot. 66) is often the most abundant plant after the fine-leaved fescues and is sometimes co-dominant with them. It is one of the fairly numerous plants which grow either on wet soil or on dry but highly calcareous soil.

Salad burnet (*Poterium sanguisorba*), with its compact heads of small purplish-green flowers and pinnate leaves with serrated leaflets, is almost constant in chalk grassland and often very abundant. It is one of the deeply rooting species, with most of the feeding roots between 16 and 27 inches long and reaching an extreme depth of 34 inches, so that it can tap supplies of water when the surface soil is very dry. It is the only characteristic chalk species which can become locally dominant among the tall grasses of temporarily ungrazed areas. The "lesser" scabious (*Scabiosa columbaria*, Phot. 65), another deep-rooted species (extreme depth 28 inches), is, like salad burnet, far more abundant and widespread on chalk and limestone soils than anywhere else, from Perth and Forfar southwards. Wild thyme (*Thymus serpyllum*), "the close-bit thyme that smells like dawn in paradise" when one is lying on a well-grazed down, is very constant and abundant, though it also occurs on other dry pastures away from the chalk.

Stemless thistle (*Cirsium acaule*, Phot. 67), with its rosette of very prickly leaves and a single dark crimson flowerhead seated in the middle of them, is another constant and abundant plant of down pasture. Of the little "purging flax" (*Linum catharticum*) with its tiny white flowers the same may be said, but it is so inconspicuous that it may be easily missed when not in flower. Burnet saxifrage (*Pimpinella saxifraga*), an umbelliferous plant with pinnate or bi-pinnate leaves, attaining some height in unpastured grassland, is another rather constant species.

Pretty constant plants of moderate abundance in chalk grassland are bird's-foot trefoil (*Lotus corniculatus*), hairy hawkbit (*Leontodon hispidus*) with its light yellow flowerheads in June turning to dull-white pappus in August

(Phot. 65), and red clover (*Trifolium pratense*). Ribwort plantain (*Plantago lanceolata*), a ubiquitous plant of neutral grassland, as we have seen (p. 146), is very constant and abundant also in down pasture. These all occur freely in other types of grassland, though not on the most acid soils.

These ten herbs occur in more than 80 per cent., most of them in more than 90 per cent., of many sample areas on the Sussex Downs, and together with the grasses mentioned earlier they form the overwhelming bulk of the herbage. Taking the first place are the fine-leaved fescues and oat-grasses, and then plants like salad burnet, thyme, bird's-foot trefoil, stemless thistle, and ribwort plantain. Some, as we have seen, are almost exclusive to chalk grassland, others are on the whole more constant and abundant there than elsewhere, while others again are quite equally common in other pastures, and these last actually make up most of the down turf.

It is among some of the less abundant species that we find most of those which are never, or very rarely, found in any other habitat.

Of the species which occur in between 60 and 80 per cent. of the sample areas the great majority are not confined to chalk, such for example as milfoil, harebell, knapweed, daisy, bulbous buttercup, self-heal, ladies' bedstraw (*Galium verum*), which is often locally dominant (Phots. 65, 68), and cowslip. On the other hand, the beautiful rampion *Phyteuma tenerum*, formerly called *Phyteuma orbiculare*, with its heads of strongly curved deep blue flowers appearing in July and August, is strictly confined to the chalk downs from Dorset and Wiltshire to Kent, and occurs in 70 per cent. of the areas examined in Sussex, where it is often very abundant. The little squinancy-wort (*Asperula cynanchica*), with 4-petalled white flowers, was found in 79 per cent. of the sample areas of Sussex chalk grassland and in England occurs almost exclusively on the chalk, frequently in great abundance.

Of less constant species, occurring in between 20 and 60 per cent. of the Sussex areas, there are dropwort (*Filipendula hexapetala*), with its tall elegant loose inflorescence and small white flowers, the flower buds a beautiful rosy pink; horseshoe vetch (*Hippocrepis comosa*), with curved

pods splitting into horseshoe segments—locally very abundant on the downs and whose bright yellow flowers turn some of the hillsides golden at midsummer; and woundwort or ladies' fingers (*Anthyllis vulneraria*), belonging to the same family, whose flowerheads are very conspicuous because of the swollen downy calyces against which the light yellow corollas are set—these three are almost confined to chalk grassland. A number of others—carline thistle (*Carlina vulgaris*), hairy violet (*Viola hirta*), upright bedstraw (*Galium erectum*), the puce-coloured gentian (*Gentiana amarella*), wild carrot (*Daucus carota*)—are commoner in this community than anywhere else.

Many other species—more than half of the whole number recorded—are only met with occasionally, and these are a very miscellaneous collection, i.e. their status is very various. Among them are some which, so far as is known, are confined or almost confined to chalk or limestone grassland. On the Sussex Downs there are at least three of these—*Senecio integrifolius*, locally quite frequent; bastard toadflax (*Thesium humifusum*), parasitic on the roots of other plants; and the rather rare man orchid (*Aceras anthropophorum*) with its greenish-yellow pendant lip, shaped like a human figure. There are a number of other orchids that are found especially in chalk grassland and never on non-calcareous soil—pyramidal orchid (*Anacamptis pyramidalis*), with its dense handsome spike of rose-coloured flowers; bee orchid (*Ophrys apifera*), local and capricious in appearance but not infrequent and sometimes very abundant; spider orchid (*Ophrys aranifera* or *sphegodes*); *Ophrys arachnites* or *fuciflora* (very rare); musk orchid (*Herminium monorchis*); dwarf orchid (*Orchis ustulata*). Other species of orchid such as spotted orchis (*Orchis maculata*) and fragrant orchid (*Gymnadenia conopsea*) are not at all uncommon, though local, on chalk downs, but they also occur in other communities. Soldier orchis (*Orchis militaris*) and monkey orchis (*Orchis simia*) are very rare plants occurring in chalk grassland and also in chalk woods. Thus there are a considerable number of orchids that may be found in chalk grassland (which is indeed the habitat of a majority of the British species), and several not at all uncommonly, while others are ex-

tremely rare; but none has a high constancy—they are always more or less local and capricious in appearance.

A very common plant of calcareous soils almost throughout Great Britain is the rock-rose (*Helianthemum nummularifolium* or *vulgare*) with widely open, rather large, light-yellow flowers and small, rather leathery, dark green leaves. This is not a regular member of the chalk grassland community, but usually inhabits chalky banks. In some, particularly rabbit-eaten, chalk pasture, however, it spreads over and becomes dominant in the grassland (Phot. 67), for it is apparently untouched by rabbits. It occurred in only 15 per cent. of the Sussex sample areas. Wild marjoram (*Origanum vulgare*) is another plant which favours the open soil of chalky banks and occasionally invades the grassland. It also occurred in 15 per cent. of the Sussex grassland areas.

Of other chalk grassland plants which are quite local the following may be mentioned: pasque flower (*Anemone pulsatilla*), very local though abundant where it occurs, mainly on the East Anglian chalk, but also on other limestones; spotted cat's-ear (*Hypochaeris maculata*), widely but sparsely distributed on chalk and limestone throughout England; the beautiful blue-flowered perennial flax (*Linum anglicum*), very local indeed, on the chalk of eastern England; the very blue chalk milkwort (*Polygala calcarea*), which is locally abundant; and the very rare *Polygala austriaca* (Kent). Common milkwort (*Polygala vulgaris*), red, white, or blue flowered, is not uncommon on the downs and also in non-calcareous grasslands such as grass heath.

Of the large number of species that are only occasionally met with in chalk grassland (e.g. in less, and often much less, than 20 per cent. of the Sussex sample areas) a few, as we have seen, are rare plants, exclusively or almost exclusively found in that community. But the great majority are either ubiquitous occasional constituents of grassland of various kinds or alien invaders of the chalk grassland community from arable land, from roadside wastes, or from woodland or wood-edges. Some of these last, e.g. wild strawberry (*Fragaria vesca*) and tufted vetch (*Vicia cracca*), occasionally establish themselves rather firmly in the grassland.

Except in the driest situations, a number of mosses commonly occur in chalk grassland, and when the herbage has a depth of 3 or 4 inches or more they often form a regular subordinate layer. By far the most constant and abundant is *Brachythecium purum*, a very common grassland moss, usually dominant in the moss layer, which is sometimes composed of this species alone. Next in importance come three species of *Hylocomium*—*H. triquetrum*, *H. squarrosum*, and *H. splendens*. These are woodland or grassland mosses of wide distribution which are present on the chalk especially in relatively damp grassland, particularly on northern exposures where they escape direct sun, and also where they are shaded by patches of scrub. Here the Hylocomia are often very luxuriant, and in heavily rabbit-attacked areas they may be dominant alone because they are not eaten (Phot. 66), while a few rabbit-resistant herbs (in this area *Carex flacca*) protrude through the moss carpet.

Next in order of frequency come a distinctly calcicolous moss, *Camptothecium lutescens*, and a very widely distributed grassland, heath, and woodland species, *Dicranum scoparium*. Less frequent are *Hypnum cuspidatum* and *Fissidens taxifolius*. A number of other species and two or three liverworts occur occasionally, and a few species of lichen are met with here and there, but these plants play no significant part in the vegetation.

The two outstanding characteristics of the chalk grassland habitat are, first, the dryness of its surface due to the thinness of the soil and the highly permeable rock below; and secondly, the high proportion of lime right to the surface of the soil, rendering the reaction normally alkaline. These two factors result in the turf being largely composed of grasses and herbs which flourish on many dry soils, and also of those which prefer or are confined to soils of constant basic reaction. Among the former are sheep's fescue, wild thyme, milkwort, and several others, while of the latter there are salad burnet, rock-rose, lesser scabious, and many less frequent species. Besides these two categories there are many species which grow in a wide range of conditions, including several "meadow-grasses" in the wide sense, such as cocksfoot, sweet vernal grass, fiorin, and

Yorkshire Fog; and among herbs other than grasses ribwort plantain, bird's-foot trefoil, and red clover. Most of these demand a fairly good supply of nutritive bases and are equally common in neutral grassland. On cool damp northern exposures damp-loving grasses occur. Calcifuges and marsh plants are, of course, absent.

Thus the down vegetation consists of a mixture of plants with different requirements, but owing to the particular combination of conditions it is very well characterised; that is, it has a considerable number of very constant species, a large proportion of which are much more often seen on the downs than anywhere else, and a few which are strictly confined to the community, in addition to the many which occur indifferently in very various grasslands. The grazing factor is also, of course, an overriding determinant, as in all pasture; and it is noteworthy that most of the chalk grassland plants can survive under the close nibbling of multitudes of rabbits, when the herbage is reduced to a height of less than an inch.

On flat and gently sloping areas the calcareous soil is often more or less extensively leached and is then invaded by heaths such as the ling and the purple bell-heather and by other calcifuge plants such as heath bedstraw, tormentil, etc., while common bent often becomes dominant. Calcicolous plants, rooted in the lower more chalky layers of soil, are mixed with the heath plants. Such areas may be called "chalk heaths." They should not be confused with the areas of true heath and scrub which are very frequent on the chalk plateaux where these are covered with "clay-with-flints," a clayey, loamy or even sandy deposit (see p. 148).

CHAPTER X

THE GRASSLANDS (*continued*)

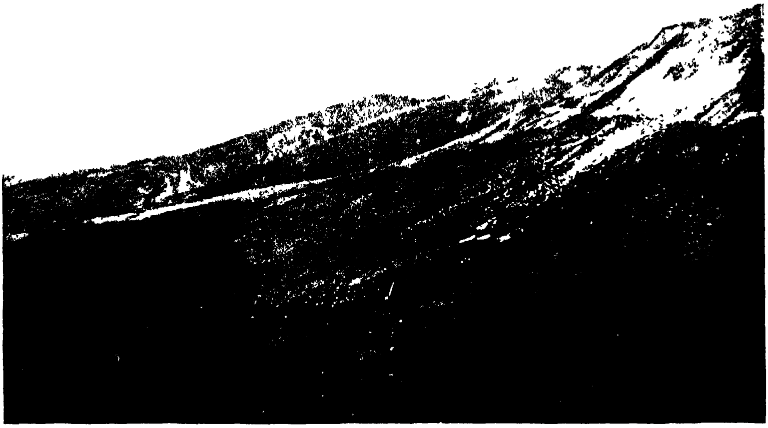
Hill Grazings, Grass Heath, and Grass Moor

THE rough hill grazings of the north and west of Great Britain are partly on the older limestones, but there is a far greater area on the so-called "siliceous" rocks—sandstones, grits, mudstones, slates, and certain schists which are very poor in lime content.

The grassland of the older (Palaeozoic) limestones resembles that of the chalk in many respects, because the essential character of the habitat—the dry basic soil—is the same. By far the most extensive of the Palaeozoic limestones is the Carboniferous [1] or Mountain Limestone, which frequently forms massive hill ranges, though some of it, for example in north Lancashire and in western Ireland, occurs in extensive tracts not much above sea level. Mountain Limestone is seen in the northern and in the southern Pennines, in north Lancashire, in North and South Wales, and in the Mendip Hills, as well as in the centre and west of Ireland.

The older limestones are much harder than the chalk and, unlike it, commonly form cliffs or crags ("scars" as they are called in the north) with screes below (Phot. 69). The thin, dry, highly calcareous soil of these is a favourite habitat of calcicolous plants, and on the smooth well-drained slopes of the limestone hills covered with grass vegetation such plants also figure largely. This limestone grassland (Phot. 69), like that of chalk, is traditional and excellent sheep-grazing, and was called "natural pasture"

[1] The Carboniferous Limestone is so called not because it bears coal but because it belongs to the same great geological period as the Coal Measures, which were formed later, after the Millstone Grit, which intervenes between them. The Coal Measures lie in basins adjacent to the massive hills of Mountain Limestone and Millstone Grit, whose strata dip below them. This is seen in the Lancashire and Yorkshire coalfields to the west of the Pennines, in the Durham and Nottinghamshire coalfields to the east, in the South Wales coalfields, and in the Bristol and Radstock coalfields adjacent to the Mendips.



Elizabeth Cowles

PHOT. 69. Limestone grassland on the steep western slope of Crossfell. Above is a limestone scar, below is heather on a grit slope.

Elizabeth Cowles

PHOT. 70. Mat-grass moor on slightly inclined flagstone slope above the scar shown in Phot. 69.

by the botanists who first studied the vegetation types of northern England early in the century. It is mainly dominated by sheep's fescue, accompanied by several other common chalk grasses, including the oat-grasses (*Avena*), *Koeleria*, and quaking-grass (*Briza*). In addition there is the strictly calcicolous blue-green grass *Sesleria caerulea*, abundant on the limestone of the northern Pennines and of the west of Ireland, much less frequent in Scotland (where limestone is comparatively rare), and quite absent from the south.

Of herbs other than grasses there are some calcicolous species, such as ladies' fingers (*Anthyllis*) and rock-rose (*Helianthemum*), which are widely spread on the limestones and on the basic igneous rocks, but many fewer than on the chalk. Some, however, such as squinancy-wort, reach the Mountain Limestone of the southern Pennines in Derbyshire, but do not go further north. Of common chalk grassland plants that are calcicolous, there are the clustered bellflower (*Campanula glomerata*), lesser scabious (*Scabiosa columbaria*), purging flax, salad burnet, horseshoe vetch, all recorded from the limestone grassland of Derbyshire and West Yorkshire, and others, such as thyme and burnet saxifrage (*Pimpinella saxifraga*), which range into Scotland.

Mixed with calcicolous and dry-soil species, however, there are, on the Mountain Limestone, some which are more or less "calcifuge," i.e. avoiding calcareous soils. Thus the common bent (*Agrostis tenuis*), which is very local in chalk grassland, is widely spread and sometimes abundant in the grassland of the older limestones, so that this may even come to approximate to the bent-fescue grassland of the siliceous hills. Tormentil (*Potentilla erecta*), which is only found occasionally on the deeper, somewhat leached, soils of chalk grassland, and heath bedstraw (*Galium saxatile*), which is quite absent from it, both occur freely in some of the older limestone areas and on the basic igneous rocks. This is a result of the cooler and wetter northern and western climate, which leads to increased leaching and formation of acid humus, so that acidity is often developed in the surface layers of soil. Where these processes are marked a whole set of heath plants may colonise the ground, sometimes leading to the strange mix-

ture of calcicolous and calcifuge plants which may be called a "limestone heath," quite comparable with the "chalk heath" mentioned on p. 157. On one such limestone heath in West Yorkshire heather, bilberry, mat-grass and hair-moss were found associated with *Sesleria*, sheep's fescue, thyme, and the yellow (or yellow-and-purple) flowered mountain violet (*Viola lutea*).

Owing to high rainfall and locally obstructed drainage the soil of Mountain Limestone, unlike the chalk, is fairly often waterlogged over limited areas, so that "limestone swamps" are produced—for example, near the foot of Ingleborough—with numerous sedges and rushes, and species like marsh marigold (*Caltha palustris*), meadow-sweet (*Filipendula ulmaria*), water avens (*Geum rivale*), grass-of-Parnassus (*Parnassia palustris*), marsh valerian (*Valeriana dioica*), etc.

The basic igneous and metamorphic rocks, such as basalts, andesites, dolerites, and various schists, produce a dry shallow soil rich in bases, especially calcium and magnesium, bearing grass vegetation very similar to that of the older limestones. In south-eastern Scotland the "laws"[1] and knolls of basic igneous rock and the basic "dykes"[2] of old lavas are conspicuous examples of such grassland, dominated by the fine-leaved fescues and containing several calcicolous species.

By far the greater portion of the hill and mountain masses of northern and western Britain are, as has been said, made up of siliceous rocks composed mainly of silica and aluminium silicates, very hard because of the enormous pressure to which they have been subjected since they were first formed some hundred millions of years ago in the Palaeozoic Age. They weather to form shallow soils very deficient in lime and other bases, a deficiency which is increased by the heavy leaching resulting from high rainfall, so that their soil reaction is commonly markedly acid. The lower slopes of these siliceous hills up to at least 1000 feet, and at times and places up to 2000, were once covered

[1] Prominent steep-sided miniature hills, conspicuous, for instance, between Edinburgh and the Berwickshire coast.

[2] Prominent ridges rising above the land on each side because the harder rock, like that of the "laws," has resisted erosion which has worn away the softer neighbouring ground.

with forest, much the greater part of which has disappeared owing to climatic changes, or has been cleared, or has been destroyed by grazing, and on plateaux often by bog formation. Since the disappearance of the woodlands the better drained slopes with less poor soils have become covered with grass vegetation created and maintained by grazing.

Above the level of valley cultivation and enclosed pasture the lower slopes of the higher hills are mainly occupied by this siliceous or acidic grassland, which frequently covers the whole of the lower hills up to a level of 1000 or 1500 feet, interrupted only by patches of relict forest or scrub, or by heath where grazing is slight or negligible. The belt of hill grazing forms the most extensive sheep pasture in our islands, but an increasing proportion is being planted by the Forestry Commission. Above the hill grassland, again, come the moorlands and bogs where peat is formed, occupying the higher gentle slopes and plateaux. In the very wet climates of the west of Scotland and the west of Ireland moorland and bog descend to sea level. Above the moorland and bog comes the arctic-alpine vegetation of the highest mountains.

The main grazings of the siliceous grassland are widely dominated by a mixture of common bent (*Agrostis tenuis*) —with which is often associated forms of the creeping bent (*Agrostis stolonifera*), sometimes replaced by another creeping species (*Agrostis canina*)—and sheep's fescue (*Festuca ovina*).

Bent-fescue grassland is not determined by altitude, since it may occur at any level below the arctic-alpine zone of the higher mountains, but by well-drained, acid, but not too poor a soil, and by regular grazing, and these conditions are usually found on the comparatively steep lower slopes of the siliceous hills. In aspect it contrasts by its brighter colour with the more neutral tints of the moorland grasses and the darker tones of the heaths, though it is not quite so vividly green as the limestone grassland. Most, if not all, of the grassland is potential woodland and was formerly covered with forest or scrub of sessile oak and birch, and patches of these trees still exist here and there side by side with the grassland under identical conditions of exposure and subsoil. Clearance of forest and scrub combined with

grazing, and probably often grazing alone, have converted the former forest and scrubland into grassland. Woodland plants such as bluebell, wood anemone, and woodsorrel are often found in the grassland, and together with bracken, under whose shade they are especially common, doubtless represent relics of the former woods. Such areas on the southern Pennines, now treeless, commonly have Anglo-Saxon or Scandinavian place-names which indicate the former existence of forest, and there is documentary evidence that in the same region, some hill spurs and terraces, which are now grassland, bore forest names in Norman times.

Bent-fescue grassland is often invaded, especially if grazing diminishes, by heather (*Calluna*) and other heath plants, and if grazing ceases altogether it may actually change into heath, reverting to grassland when grazing is resumed. This reversible reaction has been abundantly demonstrated and depends on the fact that heather cannot survive under continuous grazing, while the grasses flourish.

The soil of this grassland is typically thin over the rock below, well drained and markedly acid (*p*H 4 to 5), showing little tendency to accumulate raw humus or peat except where grazing ceases, or locally where drainage is impeded. The turf is mainly composed of bent and sheep's fescue in various proportions, more of the former in wetter and of the latter in drier situations. It has been shown experimentally that luxuriance of bent and its dominance over fescue is directly induced by increased water supply. Sheep thrive well on these pastures, though they will not support a large population and the sheep depend to a considerable extent on abundant accompanying herbs. Of other grasses *Sieglingia decumbens*, a small grass of acid soils, sometimes called "heath grass," is often present in quantity, while the almost ubiquitous sweet vernal grass (*Anthoxanthum odoratum*) is also common, but most of the "meadow-grasses" are absent. When grazing is diminished, especially during a series of wet years, the mat-grass or "white bent" (*Nardus stricta*), a coarse and almost useless grass, often invades bent-fescue grassland from neighbouring communities dominated by *Nardus* (see p. 169). Wavy hair-grass (*Deschampsia flexuosa*) generally occurs in

peaty spots. Field woodrush (*Luzula campestris*) is locally abundant.

Two of the commonest and most constant plants in bent-fescue grassland are the tormentil (*Potentilla erecta*) with its yellow 4-petalled flowers shaped like a Maltese cross and heath bedstraw (*Galium saxatile*) with narrow oval leaves and tiny white flowers. Other species commonly met with are harebell (*Campanula rotundifolia*), bird's-foot trefoil (*Lotus corniculatus*)—an important source of sheep feed—milkwort (*Polygala*), forms of wood violet (*Viola riviniana*), and often wood sage (*Teucrium scorodonia*). The beautiful yellow mountain pansy (*Viola lutea*), sometimes with its two back petals, or the whole flower, purple, is locally abundant in some hill regions of Wales and the north. There is often a great deal of moss among the herbage in winter and early spring, the commonest species being *Dicranum scoparium*, *Hypnum cupressiforme*, *H. schreberi*, and *Hylocomium squarrosum*.

Bracken fern (*Pteridium aquilinum*) is a common, gregarious, and very aggressive plant of bent-fescue grassland, often forming dense local societies, sometimes more sparsely scattered. Originally a woodland plant (see p. 82), it grows much more vigorously in full light. In certain seasons the minute wind-borne spores settle and germinate in temporarily wet spots where they can produce prothalli (the sexual generation) and ultimately new plants. In this way bracken can colonise fresh places remote from the parents. Most of the spread of the plant, however, is vegetative. The horizontal underground rhizomes, situated at various depths from a few inches to more than two feet, grow forward at the tips and branch freely, sending up a succession of fronds at frequent intervals. The rhizomes grow most vigorously in soft sands and other light soils which they can easily penetrate, such as many of those derived from the old siliceous rocks. On favourable ground the upright fronds with their obliquely ascending tough leathery pinnae are so closely set that they shade the soil very deeply from June or July, when the bracken canopy is fully developed, to October, when it withers. The soil then becomes covered during the winter with a thick layer of brown bracken litter derived from the dead fronds,

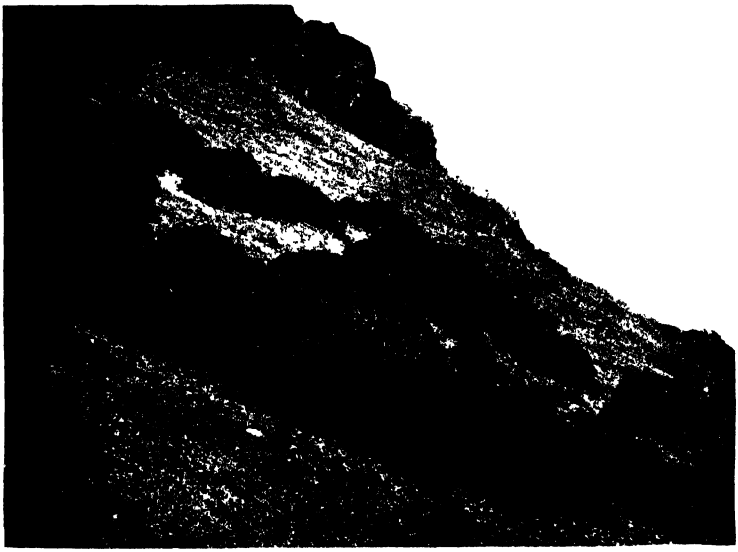
passing down into raw humus derived from the litter, and nothing else can grow beneath the densely packed fronds. In this way, as the bracken advances over rough grassland the solid mass of fronds eventually exterminates the grasses and destroys the pasture altogether. Its continuous spread over the bent-fescue pastures has seriously diminished the area available for grazing. Before bracken has attained its maximum density, however, and on less favourable ground, where the plant is weaker and the fronds are set farther apart, the grasses and herbs of the grassland can survive below the looser bracken canopy, and since this is never fully developed before mid-June they are able to vegetate in full light during the spring and early summer.

There are several factors which limit the spread of bracken. In the hill regions it is dominant only in valleys and on slopes sheltered from the more violent winds, often stopping quite abruptly as the summit of an exposed ridge is reached. Bracken ascends to 1250 feet on the Longmynd in Shropshire, to 1500 or 1700 feet on the southern Pennines, and to 2000 feet in Scotland, corresponding with the increasing height of the hill masses and the opportunities for protection at higher altitudes. Bracken cannot grow in tough heavy clay or in waterlogged soil (Phot. 71). It generally avoids highly calcareous soil and cannot flourish where the soil is trampled and compacted, so that it is excluded from well-grazed pastures and footpaths. On the other hand, when it has taken a good hold on suitable ground other plants cannot compete with it because the fronds are not eaten by stock or by rabbits, and its dense shade and thick litter prevent the growth of rivals.

Various means have been tried to combat the bracken menace, which is very serious for sheep farmers. It is often cut in autumn, since it provides good dry litter for cattle, but this does nothing to check the growth of the plant, because the fronds are then empty of reserve food, which has been withdrawn to the rhizomes. Repeated cutting of the fronds during the growing season is an effective method of starving out the plant, but the cost in labour is usually prohibitive, and a single cutting during the season is of little use. Spraying dense bracken areas with various poisons, such as sulphuric acid or sodium

Harold Jeffreys

PHOT. 71 Bracken covering a slope on a Durham fell, but stopping dead at the level ground which is wet and occupied by Yorkshire Fog.



A. G. T.

PHOT. 72. Sheep-trimmed bushes of the small western gorse in the bent-fescue pasture of the Malvern Hills.

chlorate, has been carried out, but it is expensive and troublesome and not free from danger. More recently considerable success has been obtained by the use of various machines which crush the young fronds. Where bracken has completely destroyed the pasture it is probably best to afforest the area.

Two species of the spinous gorse, furze, or whin (*Ulex*) often occur in rough grassland, forming here and there dense local societies of scrub. These are the common gorse (*Ulex europaeus*) and the smaller species (*Ulex gallii*), which occurs principally in the west, particularly the south-west. The third native species, the dwarf gorse (*Ulex minor*), is centred mainly on the south-eastern and southern heaths.

The common gorse forms a dark green bush several feet high with stout sharp stem spines and weaker leaf spines. It is mainly a lowland plant and its commonest habitats are disturbed grassland and heath where the seedlings can establish themselves on sandy or loamy soil, principally on commons and waysides and in neglected pastures. Single flowers may appear at any time from October onwards during the winter months when the weather is mild enough, but April is the month when the common gorse comes into full bloom, covering the bushes with sheets of gold in a good season. The pods dry and burst in July, scattering the hard brown shining seeds, and these are distributed largely by ants, which bite and tear at the fleshy orange "caruncle" (an appendage of the seed), dragging the seeds along the ground as they do so. This is one reason for the abundance of gorse along the sides of footpaths across commons and heaths, which the ants use as highways.

The common gorse was at one time much used as fodder. The young shoots are very palatable and nutritious, and formerly the hard old shoots were ground up in special mills and used as cattle food in many parts of the country. In north and west Wales the common gorse is said not to be native but to have been introduced for cattle fodder from Ireland in the eighteenth century, the plants being cut in every alternate year. When this use was abandoned the gorse grew up, flowered, and seeded, so that it has now spread widely along the roadsides and over the lower hill pastures, where it may be seen side by side with the native

U. gallii. It is still sometimes planted for hedges and frequently in the midlands and south for fox coverts.

Ulex gallii, the western gorse, is a more compact and lower-growing shrub than *U. europaeus*, and often occupies a zone on the western hillsides above that of the common gorse, which is mainly a lowland plant. Where the two grow together, as along many roadsides in Devon and Cornwall, and on the lower slopes of the Welsh hills, they can be distinguished not only by their somewhat different habit but by the bluer green of the common gorse and the yellower green of the western species. The flowering seasons also are entirely different. The last flowers of the common gorse are over by June at the latest, while the western gorse does not come into flower till July, and is at its best in August and September. In October, when a few flowers of common gorse sometimes begin to appear, the flowering of the western gorse is over. Thus the old saying that "when the gorse is not in bloom kissing's out of season" is only true if we take the two species together, for between them they do (or may) cover the whole span of the year; but they are never in flower together.

The western gorse in its own zone commonly forms a low scrub of rounded bushes 2 or 3 feet high, set in the bent-fescue hill pastures (Phot. 72), the form being maintained by the sheep nibbling off the soft young shoots. A similar effect is, however, sometimes produced in very windy situations by the wind drying off and killing the young shoots which try to grow out beyond the general surface of the compact bush. Gorse scrub is very often burned to clear the ground for the pasture grasses, but it has considerable power of shooting again from the basal unburned parts of the stem, at or just below the surface of the soil.

GRASS HEATH

A bent-fescue community which has many points of resemblance to the rough pastures of the siliceous hills occupies grazed sandy "common" or "wasteland" in the English lowlands. This community is often called "grass heath" because it occurs on the same kind of sandy soil

as true heath dominated by ling (*Calluna*) or purple bell-heather (*Erica cinerea*), by both of which it is commonly invaded when grazing is not too heavy. On such ground essentially the same reversible reaction occurs as on the upland bent-fescue pastures, heath replacing grassland when grazing ceases and grassland replacing heath when it is resumed.

These sandy "commons" or "heaths" are found in almost every parish where there is poor sandy soil which has not been worth cultivation. They were generally used for the more or less casual grazing of the commoners' animals, for their pasture value is low and they will not support much stock. For these reasons many of them escaped enclosure when the good pastures and the arable "common fields" were alienated and fenced.

The lowland grass heaths have a much larger and more variable flora than the hillside pastures. On the drier sandy soils in a relatively dry climate like that of eastern England there are a number of "arenicolous" (i.e. sand-inhabiting) species, some of which are confined, in Britain, to such situations. The grazed (particularly the rabbit-grazed) turf is thin and there is a good deal of open soil, easily colonised by arenicolous annuals, including "ephemerals," i.e. annuals whose whole cycle of development, from germination to the ripening of seed, is confined to a few weeks (generally in spring when the sand is still moist) and is completed before the surface sand dries out in the summer. Annual weeds of sandy arable land also easily invade such places.

Besides the generally dominant bent and fine-leaved fescues, wood soft-grass (*Holcus mollis*) may be locally dominant, and where the soil is specially acid the wavy hair-grass (*Deschampsia flexuosa*) may be found, and dry peat tends to be formed, particularly when there is local invasion of heather and the accompanying lichen (*Cladonia*, p. 177). Of other perennial grasses, sweet vernal grass (*Anthoxanthum*) is perhaps the commonest, and there are some annual grasses as well. Most of the ordinary meadow-grasses do not flourish on these poor and hungry soils.

Many of the accompanying plants are the same as those of the bent-fescue upland pastures, tormentil and heath

bedstraw being notably abundant in both, but there are a great number of others. Characteristic are the little "ephemerals," which have a very short growing season, germinating in early spring, flowering, setting seed, and drying up in the course of a few weeks. Some of them also occur on old wall tops—a similarly dry habitat: "whitlow grass" (*Erophila verna*), which has tiny white flowers with 4 deeply cleft petals, is one of the most abundant, and the little saxifrage with 3-cleft leaves (*Saxifraga tridactylites*); also parsley piert (*Alchemilla arvensis*), the changing forget-me-not (*Myosotis versicolor*), whose flowers change colour from yellow to blue, and the small grass *Aira praecox*. More local, but common on East Anglian heaths, is the cruciferous *Teesdalia nudicaulis*. Other small annuals of similar habit, which flower later, are the little bird's-foot (*Ornithopus perpusillus*) and the small cudweed (*Filago minima*). Sheep's sorrel (*Rumex acetosella*) is a very common annual on these acid soils, often dominant on patches of recently bared ground, which it colours vividly with its crimson fruits.

Of larger plants, the common ragwort (*Senecio jacobaea*) is common and very conspicuous with its showy yellow flowers. This plant is a real pest on many dry grasslands, being poisonous to stock. It has been enormously abundant in some recent years, not only on grass heaths but on chalk grassland, though it is to some extent kept in check by the striped black-and-yellow caterpillars of the cinnabar moth (*Euchelia jacobaeae*), which often strip the ragworts bare of foliage. The yellow-flowered ladies' bedstraw (*Galium verum*), with linear leaves, is another plant common to chalk grassland and grass heath, and harebell (*Campanula rotundifolia*) is yet another. The Latin name of this plant may seem a misnomer, since the stem leaves are very narrow, but the name comes from the first-formed leaves at the base of the plant, which are rounded. Yellow stonecrop (*Sedum acre*) is often found, and *Sedum telephium* (orpine, "livelong," or "midsummer men"), an erect plant with much larger, rather fleshy leaves and rose-coloured flowers, not infrequently occurs, though it is very local. The hoary cinquefoil (*Potentilla argentea*), with dark green leaves, silvery on their lower sides (a much scarcer and

more local plant than the common tormentil, *P. erecta*, which is ubiquitous on most grass heaths), is also found on these soils; also occasionally the true dog violet (*Viola canina*), not to be confused with the wood violet (*Viola riviniana*), a small form of which is very common on many grass heaths, and which is often loosely called "dog violet" because its flowers, like those of the true dog violet, have no scent. The main stem of the wood violet soon stops growing, producing only a rosette of leaves, and the flowers are borne on leafy lateral branches, while in the dog violet the flowers are produced on the leafy main axis. Species of mouse-ear chickweed (*Cerastium*) are also common, as is the field woodrush (*Luzula campestris*).

On the grass heaths of Breckland, a specially dry region in south-west Norfolk and north-west Suffolk, the poorer sands with very little exchangeable calcium bear grass heath with very few flowering plants (in the poorest of all only 9 species), of which the bents, sheep's fescue, heath bedstraw, and field woodrush are the commonest. Lichens, mainly species of *Cladonia*, form the bulk of the vegetation, usually with *Cladonia silvatica* dominant, and there are a certain number of mosses. This vegetation is very similar to that of the grey dunes (see Chapter XV, p. 244). These grass heaths are regularly invaded by heather, which easily becomes dominant when the rabbits, which are immensely abundant, are excluded. On the other hand, when a tract of heather is used as a rabbit-warren it is comparatively quickly converted into closely nibbled grass heath. The Breckland heaths are also invaded by bracken, which forms dense communities in which little else can live, and by sand sedge (*Carex arenaria*), a plant usually found on seaside sand dunes (p. 248).

GRASS MOORS

Two well-marked grass communities, forming what may be called *grass moor* because of their peaty soil, remain to be described.

Grassland dominated by the mat-grass or "white bent" (*Nardus stricta*) is a characteristic and conspicuous feature of many of our western and northern siliceous hills. It

occupies flat or gently sloping areas on the summits or shoulders of the hills above the bent-fescue pastures and bracken communities, and below the peat-covered plateaux, mainly between 1000 and 2000 feet (Phots. 73, 74, and Fig. 8). These areas stand out conspicuously from neighbouring vegetation, especially in autumn and winter, by their whitish straw colour, due to the bleaching of the massed narrow leaves of the dominant mat-grass.

Mat-grass possesses a much branched, tough, horizontally growing rhizome almost on the soil surface. This sends up leafy and flowering shoots enclosed at the base by thick tough sheaths which persist long after the leaves are dead and fallen, and then appear as double or triple comb-like series of teeth on the rhizome. The tough rhizomes and sheaths, slowly decaying, together with the remains of mosses and of the scanty accompanying herbage of other plants, form a layer of peat from 6 to 9 inches thick above the mineral soil. The thick cord-like roots penetrate this peaty layer and enter the mineral soil below. *Nardus* also settles on the loose peat worn away by rain and wind erosion from the edge of the peat plateaux above and deposited round its edges (Phot. 73 and Fig. 8), but it rarely colonises peat *in situ*. It often invades bent-fescue grazings where the drainage is poor and peat tends to be formed. Its toughness makes it troublesome and unpalatable for grazing, and it is rarely tackled by ewes or lambs. Old wethers and hill ponies eat it, but the disappearance of the wethers from the hill pastures owing to the modern taste for lamb rather than mutton has helped its increase and the consequent deterioration of the pastures. Pure mat-grass is practically useless for grazing.

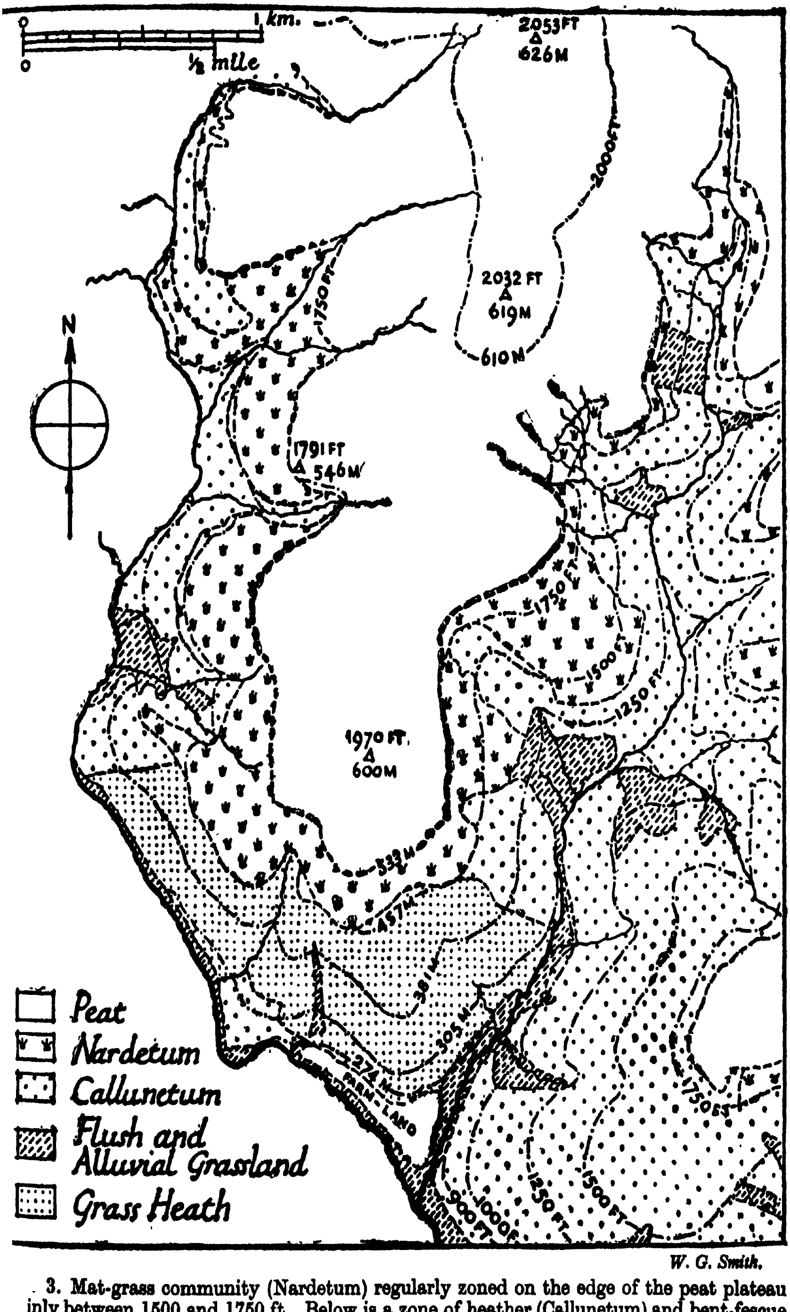
Between the tussocks of mat-grass a number of other plants are usually rooted in the thick layer of peaty humus formed by the dominant. Many of these are plants of the bent-fescue grassland such as common and creeping bent, sheep's fescue, sweet vernal grass, tormentil, and heath bedstraw. Most abundant of all is the wavy hair-grass (*Deschampsia flexuosa*), and this, especially in the southern Pennines, is often co-dominant with *Nardus*. In early summer its tall purple inflorescences, rising above the general level of the herbage, give tone and colour to the

D. Macpherson

PHOT. 73. Nardetum invading eroded edges of a peat-covered plateau. Moorfoot H south of Edinburgh.

D. Macpherson

PHOT. 74. Nardetum covering the summit of a spur in the eastern Moorfoots.



W. G. Smith.

. 3. Mat-grass community (Nardetum) regularly zoned on the edge of the peat plateau inly between 1500 and 1750 ft. Below is a zone of heather (Callunetum) and bent-fescue ssland (marked " grass heath ") interrupted by patches of better grassland in the valleys of the little streams. Moorfoot Hills.

whole grassland. Where drainage is better and the surface peat is very thin, the wavy hair-grass becomes dominant alone. On the other hand, on very gentle slopes or level ground where more peat can accumulate the mat-grass is dominant alone, sometimes almost to the practical exclusion of all other species. Besides the shallow-rooting plants mentioned above, the mat-grass peat is also colonised by peat-loving dwarf evergreen undershrubs, conspicuous among which is generally the bilberry (*Vaccinium myrtillus*), and at higher altitudes the crowberry (*Empetrum nigrum*). The common hair-moss (*Polytrichum commune*), which also inhabits damp or wet peat, is often present.

The mat-grass community is rather a dreary kind of vegetation owing to its monotony and the absence of attractive associates. It stands intermediate between the bent-fescue grazing community and the main types of peat vegetation described in the next chapter.

Another very common type of grassland in the siliceous hill regions of the north and west is Molinietum (Phots. 75-78), dominated by the purple moor-grass or "flying bent" (*Molinia caerulea*). Molinietum has many characters in common with Nardetum, which it often adjoins. Both are marginal to the main mass of peat vegetation, and both form peat on a limited scale. *Molinia*, however, requires distinctly more soil water than *Nardus* and occurs freely in many types of wet peaty soil. It forms a black muddy or brown spongy amorphous peat up to a thickness of 12 inches or so. The roots are of two kinds, "cord roots" and finer branching roots, both of which penetrate the surface peat and enter the mineral soil below. The main stem is a condensed branched rhizome from which the leaf- and flower-bearing aerial shoots arise. The leaves are long and narrow, but with a flat blade, not bristle-shaped like those of *Nardus*. The thin tapering points usually wither and turn brown during the summer, and the whole blade is deciduous. Two types of Molinietum may be distinguished —"*Molinia*-bog," in which the plant forms definite tussocks, and "*Molinia*-meadow," which is more lawn-like and of some value as pasture.

On the south Pennine moors the Molinieta are nearly pure, many stretches showing no other species, except

PURPLE MOOR-GRASS (*MOLINIA*)

T. A. Jefferies

PHOT. 75. *Molinia* sward in winter.

T. A. Jefferies

PHOT. 76. *Molinia* flush in heather.

T. A. Jefferies

PHOTO. 77. *Molinia* flushes in cotton-grass.

T. A. Jefferies

PHOT. 78. *Molinia* invading heather.

a few liverworts and algae. Where other species do occur, they are mostly peat plants. The most constant associate here, as in the Nardetum, is wavy hair-grass; bilberry is frequent, and while the common "cotton-grass" (*Eriophorum vaginatum*), and more rarely the narrow-leaved cotton-grass (*Eriophorum angustifolium*), occur in the wetter, the common heather or ling (*Calluna*) is abundant in the drier places. No other species is more than occasional in this region when *Molinia* is dominant.

Molinieta in other parts of the country are, however, richer in species, and among these, peat plants, besides those already mentioned, are commonly present: the cross-leaved heath (*Erica tetralix*), bog asphodel (*Narthecium ossifragum*), deer sedge (*Scirpus caespitosus*), and various others. Many of these Molinieta may in fact be regarded as somewhat drier parts of the peat-bog complex in which the purple moor-grass has become dominant (see p. 190). The dominance of *Molinia* seems to require a certain slow flow of fresh water with more mineral salts available than in stagnant bog. The plant is not really a typical bog plant, and it occurs in many places where the soil is quite rich in nutritive salts, as on the wet margins of many southern heaths and also on fen peat (see p. 224).

CHAPTER XI

HEATH, MOOR, AND BOG

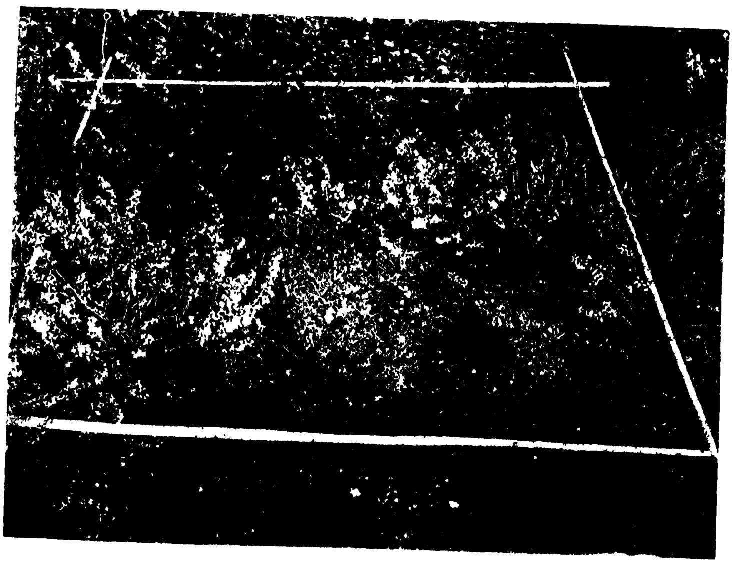
GREAT stretches of heathland are a very characteristic part of British scenery, whether the lowland heaths of the south or the upland heather moors of the north of England and Scotland. The openness and feeling of freedom on a heath, no less than the sheets of colour in late summer—the pale puce purple of the ling and the vivid red purple of the bell-heather—give a particular kind of delight and exhilaration. "The wind upon the heath" is truly "a sweet thing" in the late summer, though it may be bleak enough and the heath landscape dreary enough in the overcast days of winter.

Heath, whose vegetation is typically dominated by the common heather or ling (*Calluna vulgaris*), sometimes by another dwarf undershrub such as bilberry (*Vaccinium myrtillus*) or bell-heather (*Erica cinerea*) belonging to the same family, is one of the characteristic plant communities of the cool temperate regions of western Europe. Southwards, towards the warm temperate region of the Iberian peninsula and the western Mediterranean coasts, it passes into the evergreen shrub vegetation which the French call *maquis*. Here and there in this region, for instance on the French Riviera, heather (ling) may be found growing among the *maquis* shrubs. Northwards, in the Scandinavian peninsula, heath passes into the evergreen shrub vegetation of the Arctic tundras. The ling is a dwarf shrub, often about 2 feet high, but sometimes considerably more, with close-set, overlapping, scale-like leaves and open reddish-puce-coloured flowers.

The general European distribution of heath (*Callunetum*) follows the cool temperate oceanic and suboceanic climates pretty closely. Thus it occurs throughout the British Isles, through most of France, in Belgium, Holland, and north-west Germany, in Denmark and southern Scandinavia. Eastwards, heath vegetation becomes rarer and rarer till it disappears altogether as the climate becomes thoroughly

A. G. T.

PHOT. 79. Purple bell-heather (*Erica cinerea*) covering bared area on a heath. Birch, pine, and oak behind. Crockham Hill Common, Kent.



A. G. T.

PHOT. 80. A square metre from Phot. 79. Purple bell-heather (*Erica cinerea*) invading area in which the gravel had been laid bare. Common heather (*Calluna*) on the right. The area was first covered by a moss (*Polytrichum piliferum*) and a bent-grass (*Agrostis canina*) which are being ousted by the heaths.

S. Mangham

PHOT. 81. Oak (left), pine (left centre), beech (centre), and birch colonising heath, with heather and bracken. Ashdown Forest, Sussex.

A. G. T.

PHOT. 82. Trees which have colonised heathland: pine (left), birch (centre and right), two oaks (centre, behind), and beech (right, above). St. Leonard's Forest, Sussex.

continental, though heather itself occurs as far east as the Ural Mountains and even beyond; but there the plant is said to be confined to the shelter of woods, where it enjoys moister air.

The occurrence of heather as dominant depends on a complex of factors. The first of these is the air moisture of the cool oceanic and suboceanic climates, since it cannot flourish in severe and prolonged drought. The need for moist air generally holds for evergreen plants, except those specially adapted to desert conditions. Secondly, there must be moderately free soil drainage and a relatively high soil acidity, permitting the existence of the microscopic symbiotic fungus (*Phoma*) which infests the tissues of the heather and on which it apparently depends for well-being: this is correlated with poverty of the soil in soluble bases. Thirdly, there must be present some factor which prevents the gregarious establishment of trees that would shade the heather out. The main factors which prevent the establishment of woodland are violent winds, recurrent fires, and grazing. Fourthly, *intensive* grazing must be absent, for this quickly converts heath into grassland.

On the exposed slopes of Irish and British suboceanic hills, where violent winds are frequent, heather commonly occupies the ground up to a level of about 2000 feet, except on limestones or where there is constant grazing. These heather-clad slopes are commonest in the centre and towards the eastern side of Ireland, Wales, and Scotland, so that it looks as though a suboceanic climate were more favourable to the dominance of heather than the extreme oceanic climate of the western coasts. Heather is common enough in the wettest oceanic climates, but rarely dominant except where the soil is sufficiently permeable, or the slope steep enough, to allow of fair drainage. Under these conditions heather may become dominant on a wide variety of rocks. In wet climates heath may develop even on flat surfaces of limestone. This is because high rainfall leaches the surface layer of limestone, which is colonised by lichens and mosses so that there is an accumulation of acid humus in which heather can establish itself. Heather also becomes dominant on deep peat when it dries out. Upland heaths or "heather moors" are frequently used as "grouse moors,"

which are periodically burned to obtain fresh young growth of the heather for the grouse.

In the south-eastern lowlands heath is characteristic of the acid sandy soils produced by the sandstones of formations belonging to the Cretaceous period (Wealden sands and Lower Greensand), and also of the Tertiary and Quaternary sands, such as the Bagshot sand of the London and Hampshire basins. These soils are often too poor to be used for agriculture and have been largely left alone through the centuries. Their maintenance as heath generally depends on the prevention of invasion by trees, primarily birch and pine, and also eventually oak and beech, though certain heath soils appear to be toxic to tree seedlings. The colonisation of heath by these trees is shown in Photographs 79, 81, and 82. The young trees are, however, frequently destroyed by the recurrence of fires, mainly accidental, which in dry summers sweep across the heaths. In an early stage of development, while the heather is still young, many of the ling plants are not killed by fire and recovery is rapid. On an old heath the massive accumulation of combustible material produces great heat and all the heather may be destroyed. Full recovery then takes place in about twenty years, the burned area being reseeded from surrounding tracts of heath. Any young trees which may have invaded the area are, of course, destroyed by the fire, but if such a heath remains unburned for long enough it will be increasingly occupied by trees, which eventually shade out the heather and establish woodland. In regions where there are few trees, however, such as those near the coast of East Anglia, heaths may remain uncolonised indefinitely owing to the absence of the necessary seed parents.

The sandy soil of these southern English heaths is more or less podsolised (see pp. 88, 89) and often shows the typical stratification of a podsol. On the surface is a layer of dry peat, very frequently only an inch or less in thickness; but with a high rainfall, as on the top of Hindhead in Surrey (900 feet), it may reach a thickness of 12 inches, as it commonly does on the northern and western heather moors. Below this is the bleached layer of sand (*A*), sometimes dead-white owing to the complete removal of iron

salts, and below this again a dark brown, sometimes black, layer of "pan" (*B* 1) composed of compacted humus material which has been carried down from the surface. Underneath the humus pan a reddish layer (*B* 2), rich in iron salts, may often be distinguished before the unaltered sand or subsoil (*C*) is reached.

Most of the surface dry peat is formed by lichens of the genus *Cladonia*, of which the ground layer of the Callunetum is largely composed. With the lichens are mosses (such as *Polytrichum juniperinum*, *Hypnum cupressiforme* var. *ericetorum*, *H. schreberi*, *Dicranum scoparium*); and these, together with the dead twigs of the heather, contribute to the formation of the peaty humus.

One of the commonest plants accompanying the ling is the purple bell-heather (*Erica cinerea*, Phots. 79, 80), which has handsome bell-shaped flowers constricted at the mouth, brighter and redder than those of the ling, and short bristle-like leaves. It is often dominant on dry sunny slopes where there is less humus, and is conspicuous also while the Callunetum is regenerating after a fire that has been severe enough to destroy the peat and lay bare the mineral soil below, and again where heath is developing on bared gravel or sand (Phot. 79). In other words, *Erica cinerea* prefers a drier soil than *Calluna*. The cross-leaved heath (*Erica tetralix*), with waxy rose-coloured flowers, also constricted at the mouth, is sometimes found scattered through a damp Callunetum but is more abundant in wet heath and in bogs (pp. 179, 186, 190). Another member of the same family often found in the Callunetum is bilberry (*Vaccinium myrtillus*), with flat deciduous leaves. In the south of England this is rather a local plant, in contrast with its widespread dominance in the north. In dense Callunetum it may form a subordinate layer beneath the shade of the ling, and in that position it does not flower.

On the southern heaths the dwarf gorse (*Ulex minor*), which, like the western gorse (*U. gallii*, p. 165), flowers in the late summer and early autumn, is locally very abundant. It occurs in two forms, one a prostrate or semi-prostrate plant with short weak spines and very small flowers, the other an erect plant 2 or 3 feet high with stronger and longer spines. The prostrate form may grow as an under-

storey to the dominant heather or in intervals between the *Calluna* plants; the larger forms small clumps of dwarf spiny scrub. The gorse generally survives even very hot fires, shoots again from the base, and is prominent during regeneration of the Callunetum.

The common gorse (*Ulex europaeus*) and its role in vegetation have already been described (p. 165). It is not a true member of the heath community, though it readily invades heathland which has been disturbed, and often lines the sides of tracks across a heath.

Bracken (*Pteridium aquilinum*), again, does not as a rule seem able to invade undisturbed heath in which *Calluna* is fully established, though scattered dwarf fronds of bracken are often seen in Callunetum. It is probable that in such cases the rhizomes of bracken had penetrated the area before the ground was fully occupied by the heather, with which the bracken now maintains itself in competition. That it has some difficulty in doing so is indicated by the sparseness and comparative smallness of the fronds, and by the fact that dead bracken rhizomes may often be found below the surface layer of dry peat. It seems that the bracken rhizomes growing under these conditions are enfeebled and sometimes killed, perhaps because the layer of sand in which they grow is very poor in nutritive salts, or because adequate aeration is cut off by the impermeable layer of dry peat above. In Breckland, however, where the sandy soil is very loose and the surface layer of peat thin, it has been found that bracken can successfully invade and destroy Callunetum in which the heather bushes and clumps are not in lateral contact. The fronds shoot up between and through the heather, and when they wither in autumn and fall over on the bushes the heather is smothered and eventually killed.

Pure dense Callunetum has very few associated species beyond those already named. Broom (*Sarothamnus scoparius*), with large light yellow flowers, is not uncommon, and the small spiny undershrub, petty whin (*Genista anglica*), is found on some English heaths. In the intervals between the bushes of heather in a loose community a few grasses occur, such as common bent (*Agrostis tenuis*), wavy hair-grass (*Deschampsia flexuosa*), and *Sieglingia decumbens*. The pill

sedge (*Carex pilulifera*) is often found, and also the tormentil and heath bedstraw, ubiquitous on light acid soils, while the hard fern (*Blechnum spicant*) occurs on the damper heaths.

On areas of lowland heaths where the soil is constantly waterlogged there is a distinctive community. This wet heath shows a collection of plants essentially similar in composition to those of the bog communities described later in this chapter, but without many of the structural and developmental features characteristic of the extensive western and northern bogs. *Calluna* may be present in the drier parts of wet heath but is never dominant. In the wettest places bog moss (*Sphagnum*) may be dominant, and various other mosses are usually present. Other characteristic species are the insectivorous sundews (*Drosera*), bog asphodel (*Narthecium ossifragum*), bog pimpernel (*Anagallis tenella*), several species of sedge (*Carex*), beaked sedge (*Rhynchospora alba*), and the insectivorous butterwort (*Pinguicula*). The most constant species in this community is cross-leaved heath (*Erica tetralix*), which is often dominant in a zone towards the edge of the wet area. Another wet-heath species is *Erica ciliaris* (Phot. 83) with beautiful rose-coloured flowers, confined to single localities in Dorset, South Devon and Cornwall. On the edges of wet heath, too, purple moor-grass (*Molinia caerulea*) is often present, a grass which, as we have seen (p. 172), dominates considerable areas of grass moor in the north and west, and occupies the drier edges of the great western bogs of Scotland and Ireland.

The upland heaths and heather moors occur on the old hard non-calcareous rocks of the west and north, generally at elevations of 1000 to 2000 feet, i.e. above the zone of farmland. A distinction is sometimes made between heaths and heather moors, based on the damper and thicker peat of the latter, but almost the only vegetational difference is the greater number of rather rare species of liverworts and lichens on the "heather moors" owing to the wetter climate or wetter local conditions. The upland, like the lowland, Callunetum is poor in species of flowering plants, and the commonest are nearly the same, but there are distinctive species in the west, and others in the north, which are not found on the south-eastern lowland heaths.

In the west there is the grass *Agrostis setacea*, a species with bristle-like leaves, common on the western heaths, and the western gorse (*Ulex gallii*), which is very common on western heaths, taking the place of *U. minor* on the south-eastern, besides forming scrub on the bent-fescue grassland (p. 166). Besides *Erica ciliaris* (Phot. 88), already mentioned, the brilliant lilac-flowered "Cornish heath" (*Erica vagans*, Phot. 82) is restricted, in Britain, to the serpentine rock of the Lizard peninsula. All these have their main centres of distribution near the more southerly Atlantic coasts of Europe.

In the north a number of dwarf shrubs, several belonging to the heath family (*Ericaceae*), play a considerable part in heath vegetation associated with ling, and at higher altitudes in its absence. Bilberry (*Vaccinium myrtillus*), called in Scotland "blaeberry," with its delicious blue-purple fruits, is abundant on many of the upland heaths, largely in company with heather, to which it often forms an understorey, as on some of the southern heaths. But it also dominates communities on rocky edges ("bilberry edges") and summits ("bilberry summits"), as well as extensive areas of moor ("bilberry moors") above 2000 and up to 3000 feet where heather is sparse or absent. Cowberry (*Vaccinium vitis idaea*), with red berries, acid and not very edible, is also locally common in the north, and in places dominant, especially at the higher altitudes. *Vaccinium uliginosum* is a procumbent species of high altitudes, with berries like bilberries but smaller. Bearberry (*Arctostaphylos uva ursi*), with trailing branches and red drupes,[1] is often abundant or even locally dominant towards 2000 feet and above. Alpine bearberry (*A. alpina*) is a rare species of dry mountain heaths in Scotland, with deciduous leaves and black drupes. Two other dwarf shrubs not belonging to the heath family, namely crowberry (*Empetrum nigrum*), with crowded heath-like leaves and shining black globular fruits, and cloudberry (*Rubus chamaemorus*), allied to the brambles, with large white flowers, rather large lobed leaves and delicious orange-coloured fruits, are almost entirely northern, though there is a little crowberry in the south-

[1] A drupe is a fleshy fruit with a hard "stone" round the seed. Plums and cherries are familiar examples of drupes.

Elizabeth Cowles

PHOT 83 *Erica ciliaris*, a rare species of boggy ground in Dorset and Cornwall Near Perranwell, Cornwall.

J Massart

PHOT 84 The Cornish Heath (*Erica vagans*) and small western gorse (*Ulex gallii*) on the Lizard Peninsula *Erica vagans* is confined to the serpentine of the Lizard.

west. It will be noted that all of these dwarf shrubs, unlike the heaths proper (*Calluna* and *Erica*), bear berries or drupes, i.e. fleshy fruits, and most of them are valuable food for grouse and black game. Only bilberry and cloudberry are regularly used by man, though cowberries are said to be sometimes sold as cranberries. True cranberry (*Oxycoccus palustris*) is a bog plant (p. 186). The dwarf birch (*Betula nana*), which grows no higher than the heath undershrubs among which it occurs, is almost confined in Britain to the high-level bilberry moors of the Scottish Highlands.

A number of herbs also are either confined to the northern heaths (and woods) or are much commoner in Scotland. Among them are the species of wintergreen (*Pirola*)—also belonging to, or at least allied to, the heath family—some of which do occur in the south of England, but all are mainly northern, inhabiting heaths or old woods. They are perennial plants with white or pinkish flowers and shining evergreen leaves. Chickweed-wintergreen (*Trientalis europaea*), belonging to the primrose family, is another evergreen herb with white flowers abundant in many Scottish woods and heaths. The lesser twayblade (*Listera cordata*) is an orchid not uncommon under heather in Scottish pinewoods and heaths, but very rare in the south. The dwarf cornel (*Cornus suecica*) is a little herbaceous plant allied to the common dogwood, with a group of tiny purplish flowers surrounded by four white bracts simulating the petals of a flower. It is nearly confined to Scottish bilberry moors at higher altitudes. Clubmosses (*Lycopodium*), especially *L. clavatum*, are also common on many northern heaths and moors but are quite rare in the south.

The upland heaths or moors, ranging in altitude from 1000 to as much as 3000 feet, cover great areas on the north English, Irish, and Scottish mountains. Those dominated by heather are most numerous in the centre and towards the east. Some are developed on sandy or gravelly soils, in Scotland often on the gravelly moraines of old glaciers, with a minimum of surface peat formation (also the habitat of self-regenerating native pine woods, p. 124), others on impermeable soils on which deep peat is formed, but whose surface is relatively dry. The former often show typical

podsol structure. In common language they are all called "moor" or "moorland," words which are applied to any open tract of "waste" land, particularly at a high elevation, which is not good pasture like the limestone or the bent-fescue grasslands. This means that the soil is markedly poor in mineral bases and acid in reaction, the humus accumulating and forming compacted *mor*, i.e. acid peat—a thin layer under dry, a considerable depth under damp conditions. Such acid peat soils bear a wide range of communities—from heather and bilberry on the drier peat, through the grass moors dominated by mat-grass (*Nardus*) or purple moor-grass (*Molinia*) described on pp. 169-178, to the wetter peats dominated by deer sedge (*Scirpus caespitosus*) or cotton-grass (*Eriophorum vaginatum*) and bog moss (*Sphagnum*). These last are more usually known as "moss" or "bog," but have sometimes been called "wet moor."

A great deal of the moorland is not dominated by a single species but shows a mosaic of different dominants or a mixture of the species mentioned above. This is often due to the diversity of the terrain: a rocky outcrop with thin soil, for example, being covered by heather and bilberry; a moist peaty slope by *Molinia*; a waterlogged area of deep peat by deer sedge or cotton-grass or both together, with patches of bog moss and accompanying plants here and there. There is also evidence of changes in the moorland vegetation, sometimes due to drainage, sometimes to changes in grazing and to burning. These changes have not been studied closely enough to allow of an account of the effects of the different factors, but some of them clearly make for the establishment of drier soil conditions with consequent alterations in the vegetation. Mixtures of different dominant species are to be expected while such changes are taking place.

While it is the upland heaths, heather moors, and some of the bilberry moors that are mainly used for preserving grouse, enormous areas in the Highlands are devoted to red deer for stalking. These "deer forests" occupy the moorland slopes and upland valleys and extend over the summits of the small mountain complexes which make up the Scottish Highlands. In the summer the deer roam over the

moors and feed on the growing shoots of young heather and on the grasses; in winter they descend into the valleys, and wherever they can find woodland they feed on the twigs and bark of the trees, with any nut-like fruits such as hazel-nuts, beech-nuts, and acorns they can get. There are little more than fragments of native birchwood, with remains of existing native pine in places, within the area of the deer forests themselves, and the regeneration of these is almost entirely prevented by deer eating off the seedlings and saplings. New plantations have to be carefully fenced against deer. In a hard winter the deer attack farm crops and even come into the gardens of houses in the valleys, and most of the herds have to be fed by hand to keep them alive. All this is the result of overstocking deer forests, together with severe depletion of the woodlands. In their natural state the red deer, which in central Europe are forest animals, require woodland for their subsistence in winter, though they live well enough on the moorland in summer; and under natural conditions an equilibrium between the deer and the vegetation would be established. But if such an equilibrium is to be produced, and the deer are to remain in any numbers, more woodland in the valleys is essential.

Over much of the moorland sheep and occasionally cattle —now in comparatively small numbers—are grazed, but these are but a small fraction of the great flocks that were maintained on the Highland sheep-runs in the great sheep-farming era of the late eighteenth and early nineteenth centuries, before the immense artificial increase in numbers of the deer, and the formation of extensive deer forests. The reduction of grazing has resulted in the increase of moorland plants at the expense of good pasture.

BOG VEGETATION

We now turn to consider the bog vegetation, whose centres are in the high rainfall districts of western Scotland and western Ireland, though it may develop in other parts of these islands under appropriate local conditions.

The word bog is often used in common language for any ground so saturated with water that the foot sinks into it, but in the study of vegetation it has become customary to

restrict it to the kind of wet ground, so well known in Ireland, which bears bog moss and the associated plants. The soil is wet acid peat, and the vegetation so characteristic that it can be recognised at a glance, and not only by the expert eye. In the north of England and in some parts of Scotland the bogs are commonly called "mosses," probably because they were at one time dominated by bog moss (*Sphagnum*), as some still are.

Three kinds of bog may be distinguished: valley bog, raised bog, and blanket bog. The areas of wet heath described on p. 179 are mostly examples of small *valley bogs*, occurring in local depressions of the heathland where the water is held up by impermeable soil below. The valley bogs of the wet climate of the west and north are developed along the courses of streams draining acidic rocks where the flow of water is obstructed, as on the flat bottoms of valleys, so that the stream tends to spread beyond its course and keep the adjacent ground wet, while the heavy rain falling on it cannot run off freely into the stream. Here bog moss appears, peat is formed, and the characteristic bog vegetation develops. This, however, contains plants, such as common rush (*Juncus effusus*), various sedges (*Carex*), and the species of hair-moss (*Polytrichum commune*) which grows in wet places, not found in the purest bogs. The reason is probably that the stream water brings a certain quantity of soluble salts from its upper reaches where erosion is taking place, so that it is not so poor in salts and is less acid than the water of the purest bogs.

Raised bog is sometimes developed on the top, so to speak, of a valley bog, by the continuous growth of peat raising the surface above the level of the stream, encroaching upon its bed and generally obstructing its course. Often the bog vegetation actually bridges over a narrow stream, at the same time diverting part of the current to one side of the bog, or forcing it to split into two portions which find their way round the bog and rejoin at its lower end, while part of the water may follow its original course below the overarching peat. Sometimes deep holes with running water at the bottom may be seen in the middle of a bog at points where the covering has not been complete.

Many raised bogs, however, such as those of the central

Irish plain, have been developed in shallow basins on the top of fen (see p. 227). Fen itself (Chapter XIV) has an alkaline or neutral ground water, in which most species of *Sphagnum* cannot possibly grow; but the large tussocks of certain fen plants, rising above the water level, produce, by the decay of their leaf bases, an acid humus out of reach of neutralisation by the ground water, and this is frequently colonised by bog mosses. In a suitable climate such colonies of *Sphagnum* may spread far and wide over the fen, joining to form a typical raised bog in which the characteristic acid-loving bog species occur, obliterating the fen vegetation, and building up bog peat above it. Bores sunk through such a raised bog reveal fen peat at the lower levels, and as much as 15 feet of bog peat alone may be formed on the top of it. Raised bog may thus come to occupy the whole of an original fen basin; or, on the other hand, a fringe of fen may still surround the bog, along the edge of which the diverted original stream, or part of it, still flows.

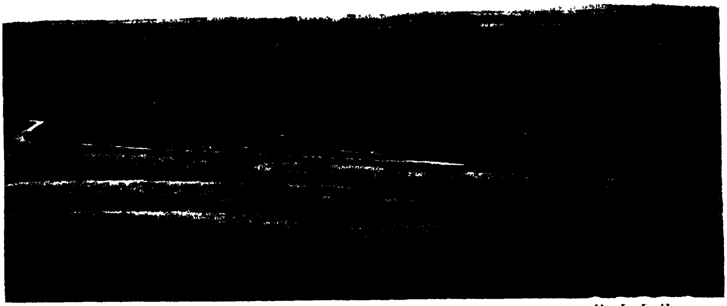
Raised bogs are very frequent in the central plain of Ireland (Phot. 85), having been formed in the numerous shallow basins, many of which were originally occupied by lakes formed on the highly calcareous glacial drift derived from Carboniferous Limestone and left when the last Pleistocene ice sheets disappeared. These lakes were gradually colonised and obliterated by fen vegetation, in course of time superseded by bog. The raised bogs of central Ireland are known as "red bogs" from the reddish-brown colour of their massed vegetation, contrasting with the bright green of the grassland on the surrounding calcareous soil. They are the great source of the peat fuel on which the population almost wholly depended for many centuries. Some idea of the enormous aggregate of peat produced in these bogs may be gathered from the fact that until very recently the peat had been taken only from the edges of most of them, and few had been completely destroyed, though quite untouched bogs were hard to find.

In their natural state, and while they are still growing, raised bogs have a convex surface, sloping very gently from the centre towards the edges, terminating in a more abrupt slope to the marginal watercourse or *lagg* (a Swedish term),

which is commonly fringed on its outer side by fen vegetation. In most old bogs a wide zone towards the edge is occupied by more or less static vegetation, the central portion alone still growing actively. This actively growing part of the bog (technically called the "regeneration complex") has a most characteristic structure, consisting of small hollows containing pools of water in wet weather, alternating with intervening hummocks (Phots. 86, 87), and a close examination of these reveals the way in which the bog is built up.

The bottom of a wet hollow and the lowest zone of its side are lined with a bright green semi-aquatic species of bog moss—*Sphagnum cuspidatum* (Phot. 88) with only an occasional vascular plant. At the bases of the hummocks the moss carpet is colonised by vascular plants, of which the white beaked sedge (*Rhynchospora alba*) is usually dominant, associated with bog asphodel (*Narthecium ossifragum*) with bright yellow, and cross-leaved heath (*Erica tetralix*) with rose-coloured, flowers. Narrow-leaved cotton-grass (*Eriophorum angustifolium*) occurs commonly in this zone (Phot. 88). A little higher up the side, bog asphodel and cross-leaved heath are frequently dominant. Two striking plants may be found about this level, both belonging to the heath family—cranberry (*Oxycoccus quadripetalus*), with its long lanky stems and bright-red astringent edible berries, and *Andromeda polifolia*, with rather large, leathery, pointed leaves and capsular fruits.[1] *Sphagnum papillosum* now begins to replace *S. cuspidatum* in the moss layer below the flowering plants and often forms the bulk of the hummock, while common cotton-grass (*Eriophorum vaginatum*) and deer sedge (*Scirpus caespitosus*) often become generally dominant at this level. These two tufted plants with long filiform leaves are superficially very much alike, and they are often so conspicuous and abundant as apparently to dominate the whole bog at a casual glance. The upper part of the hummock is formed by bog mosses which do not require so much moisture, very often the crimson *Sphagnum rubellum*. Here *Calluna*, isolated plants of which occur in lower zones, becomes dominant, and its common associate, the lichen *Cladonia silvatica*, appears

[1] A capsular fruit is a dry fruit which opens to liberate the ripe seeds.

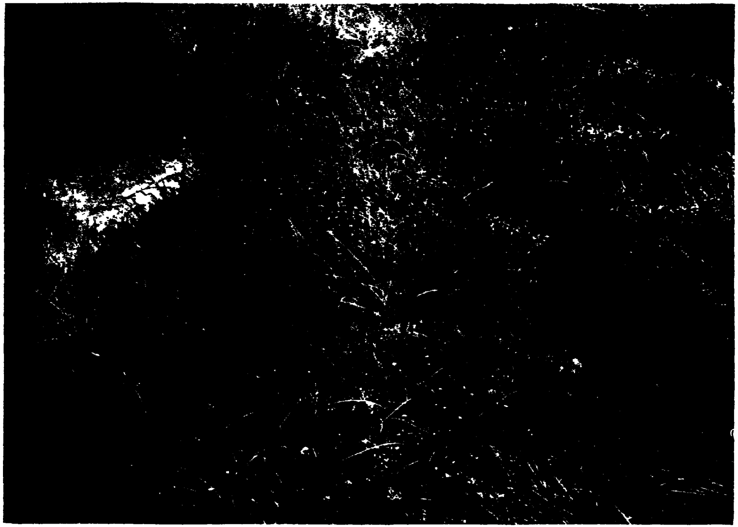


R. J. Lythgoe

PHOT. 85. Raised Bog near Shannon Bridge in the central Irish plain, from the top of a neighbouring esker. The dark zone beyond the road on the cut edge of the bog is covered with heather.

R. J. Lythgoe

PHOT. 86. Raised Bog at Kilsallagh. West Meath. Surface of "regeneration complex" showing hollows and hummocks. The hummocks are composed of bog moss (*Sphagnum*) and crowned by the lichen *Cladonia* (white in the photograph). The tufted plants with narrow leaves are cotton-grass and deer sedge. Heather is abundant.



R. J. Lythgoe

PHOT. 87. Two hollows (pools) with hummock between, on raised bog near Edenderry. *Sphagnum cuspidatum* in pools, hummocks of *S. papillosum*, etc. Cotton-grass, deer sedge, cross-leaved heath and heather are seen on the hummocks.

R. J. Lythgoe

PHOT. 88. Close view of hollow and adjacent hummock. The hollow in front is filled with *Sphagnum cuspidatum* in which narrow-leaved cotton-grass (*Eriophorum angustifolium*) is growing. The dark hummock of bog moss behind is capped with the light-coloured lichen *Cladonia*. Heather in flower on each side of the hummock.

Face p. 187

(Phot. 88). The summit of the hummock eventually dries out, the bog moss dies, the heather becomes old and leggy, and finally also dies.

The actual surface of an actively growing bog is a mosaic of very small areas bearing these different phases of vegetation. Besides the wet hollows and the fully developed heather-covered hummocks, there are intermediate patches dominated by bog asphodel, cross-leaved heath, cotton-grass or deer sedge, on incompletely developed hummocks.

The striking and very constant zonation in space just described represents a real succession of plant communities in time, from the bottom of the wet hollow in which *Sphagnum cuspidatum* is dominant, through increasingly dry stages, to the top of the hummock where no bog moss can any longer exist. The peat of the wet hollow, originally formed entirely by *Sphagnum cuspidatum*, becomes somewhat drier as it is built up, and begins to be colonised by flowering plants, and by other species of bog moss, till with constant accumulation of peat a new hummock is formed in place of the original hollow. Meanwhile the growth of neighbouring hummocks has slowed down and eventually ceased, so that they are finally overtopped by the new hummocks. Thus new hollows are initiated in place of the old dried-out hummocks, and these collect water and are duly colonised by *Sphagnum cuspidatum*, starting the cycle afresh.

This mode of bog development results in a lenticular structure of the peat of a raised bog (Fig. 4), and the reality of the succession is confirmed by vertical borings through the peat. In one such boring through an Irish raised bog, four complete cycles of peat formed in the development of hummocks from hollows were passed through, together with an incomplete cycle, and an irregular one which may have represented parts of more than one—at least six cycles in all. The bottom of the lowermost (first) cycle lay at a depth of 4·5 metres (about 15 feet), the level at which the bog was initiated. Below this level were two metres of fen peat and then more than a metre of reedswamp peat, underlain by more than one and a half metres of cream-coloured marl deposited on the bottom of the lake on the site of which fen, and thereafter the bog, had developed. Thus the depth

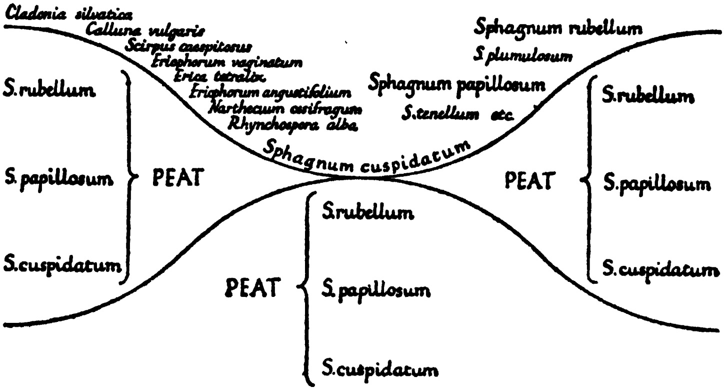


FIG. 4. Diagrammatic section through the surface of a Raised Bog. A current hollow with two adjacent hummocks is shown at the top. The succession of species of bog moss is shown on the slope of the right-hand hummock, and of species of flowering plants on the slope of the left-hand hummock. The main layers of bog moss peat which build up the hummocks are shown below and at the sides.

from the surface of the bog to the bottom of the original lake was about 80 feet.

When a bog stops growing, as it apparently does first towards its circumference, the formation of hummocks of course ceases; and since there is no longer a sharp contrast between wet and dry habitats, the surface becomes occupied by a more or less uniform vegetation in which cotton-grass or deer sedge, or both together, are usually dominant, with a mixture of heather. At the extreme edge of the bog, where the drainage is much freer, there is a narrow belt of dominant *Calluna* (Phot. 85), which also commonly occupies the steep marginal slope. This slope is sometimes colonised by gorse or broom, and occasionally by birches or pines.[1] When an Irish bog is drained its surface always becomes covered with heather.

Raised bogs are now far commoner in the central Irish plain than anywhere else in the British Isles, but there are still a small number in north-west England and south-west Scotland. Most of the English bogs have been drained or destroyed, but a very good active one (Tregaron Bog) still exists in central Wales.

[1] In the more continental climate of Sweden raised bogs are often eventually fully colonised by pines.

Elizabeth Cowles

PHOT. 89. The blanket bog of Connemara with low heather-covered outcrops of rock appearing through it. "The Twelve Pins" in the distance.

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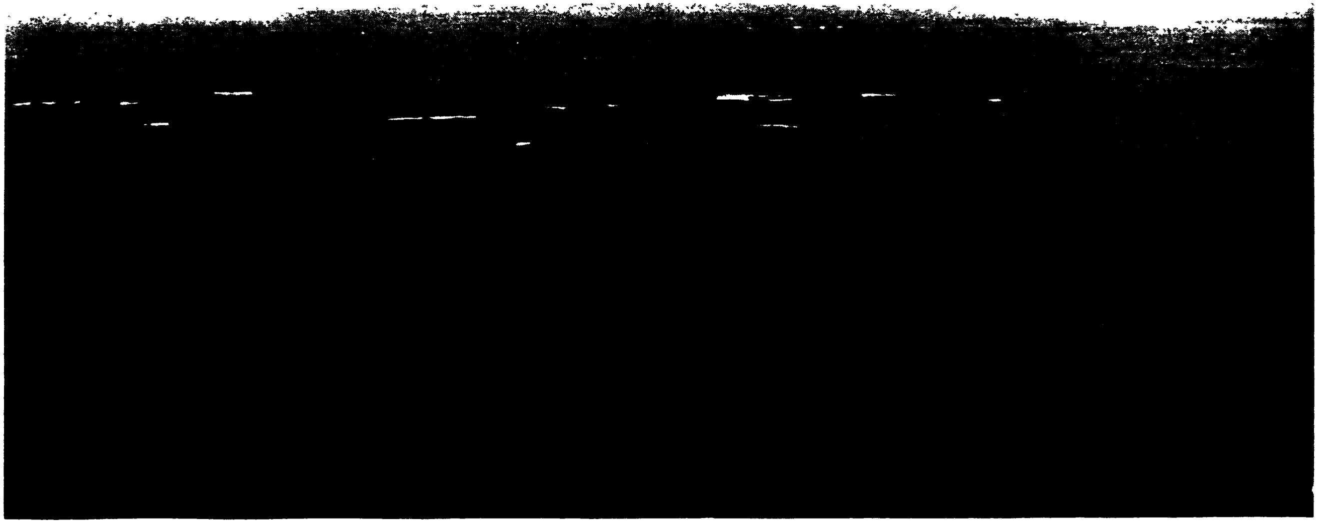
BLANKET BOG



R. J. Lythgoe

PHOT. 90. The blanket bog of western Mayo, with bog pools. This photograph gives a good idea of the vast monotony of these bogs, especially on a misty day such as that on which it was taken.

Blanket Bog

Blanket bog is a characteristic formation of the very wet climate of western Scotland and western Ireland. It is so called because it covers the countryside like a blanket, except in places with really good drainage, such as steep slopes, rocky outcrops, or highly permeable soils. The vast bogs of Connemara and western Mayo in Ireland (Phots. 89, 90), and of parts of Argyll, Ross, and Sutherland in western Scotland, are typical examples of blanket bog, and somewhat similar vegetation covers the almost level high-lying plateaux of many of the Scottish and north English hills such as the Pennines, as well as similar tracts in Wales and on Dartmoor in the south-west.

The common character of these regions is the very wet climate, not only high rainfall, but almost constantly damp air for the greater part of the year, not counteracted by adequate drainage, so that the soil and vegetation remain wet for most of the time because the water cannot escape by percolation or run off, nor can it evaporate freely.

Blanket bog is not sharply separable from peat moor, because the diversity of climate, slope and soil leads to every degree of wetness of the ground. Accordingly we find infinite variation in the dominance and mixtures of different species, as already described (p. 182), from the dominance of heather at one extreme, through that of *Molinia*, to the dominance of deer sedge or cotton-grass, and finally of beaked sedge or bog moss, at the other. It is the communities composed of these last plants, where the foot sinks into the wet peat, that are properly spoken of as bog.

The plants of blanket bog are mostly the same as those of raised bog, since the general features of the wet acid peat habitat are substantially the same. *Molinia*, however, is nearly always present, at least on the edges of blanket bog, while it appears to play no part in raised-bog development. *Sphagnum* is not nearly so universal as it is in raised bog, though there are always local patches dominated by bog moss. The species of *Sphagnum* are on the whole the same as those of raised bog. The relations of bog moss to the development of blanket bog are not, however, fully understood, since very little close study has as yet been given to it. It is probable that an alga (*Zygogonium ericetorum*), characteristic of acid soils, first colonises the wet ground,

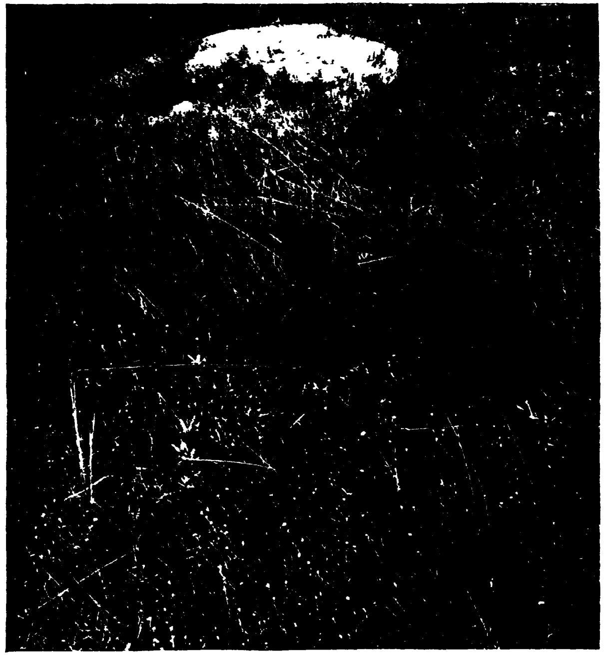
and is followed by *Sphagnum cuspidatum*, which in its turn is followed by the white beaked sedge (*Rhynchospora alba*, Phot. 92), as in raised bog. This plant commonly dominates areas of the wettest peat. Associated species in the Connemara blanket bog are bog asphodel (*Narthecium*), sundews (*Drosera*), and cross-leaved heath (*Erica tetralix*), the last named extending freely to somewhat drier parts of the bog; and here, especially on shallow peat, it is often accompanied by the closely allied *Erica mackaiana* and by the rare and local St. Dabeoc's heath (*Dabeocia polifolia*), with large handsome rose-coloured flowers. These two are absent from raised bog, as are a number of other species found in the Connemara bogs, such as bog myrtle (*Myrica gale*) and broad-leaved cotton-grass (*Eriophorum latifolium*). Common cotton-grass (*E. vaginatum*) and the narrow-leaved species (*E. angustifolium*) are also frequent or abundant, together with deer sedge (*Scirpus caespitosus*), but none of these is dominant over any considerable tract of west Irish bog. A plant which is frequently abundant or dominant in the wetter parts of the Connemara and Mayo bogs, often associated with *Rhynchospora*, is the black-headed sedge *Schoenus nigricans* (Phot. 92). This is also found in Scottish bogs and on wet heaths in Cornwall near the coast, but in England it is most characteristic of calcareous fens. It has been conjectured that sea salt in the spray blown on to coastal bogs by the wind may render them somewhat alkaline.

Purple moor-grass (*Molinia caerulea*) is very abundant and practically ubiquitous in the drier tracts of the west Irish bogs. This is a plant with a very wide range of habitat. It dominates, as we have seen (pp. 172, 178), considerable tracts of wet mineral or peaty soil on the edges of the main mass of upland peat vegetation. It is also common in the wetter parts of English lowland heaths, besides occurring on calcareous fens (p. 224); but it is absent from actively growing typical raised bog.

Deer sedge (*Scirpus caespitosus*) is rarely dominant in the west Irish blanket bogs, though it is commonly present. On the other hand, it dominates the higher plateaux of the Wicklow Mountains south of Dublin, and covers wide tracts of the blanket bogs of the north-west Highlands. A very

R. J. Lythgoe

PHOT. 91. Bog pool with bog bean (*Menyanthes*) in the water, and hummocks capped with the moss *Rhacomitrium*, in the western Mayo blanket bog.



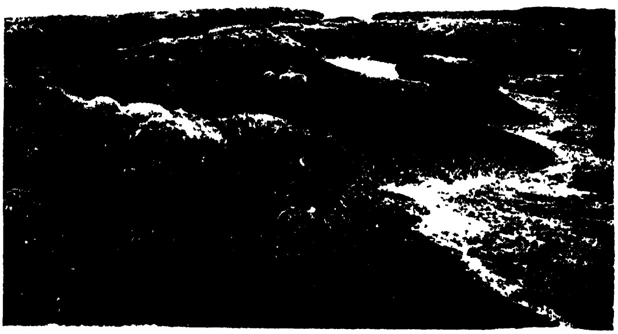
R. J. Lythgoe

PHOT. 92. Connemara blanket bog. White beaked sedge (*Rhynchospora*) in foreground, black-headed bog-rush (*Schoenus*) behind. Large hummock capped with the white moss *Leucobryum* in the distance.

Face p. 190

W. B. Crump

PHOT. 93. Cotton-grass (*Eriophorum vaginatum*) in fruit (June), on the peat plateau near Huddersfield.



A. Wilson

PHOT. 94. Eriophoretum dissected by streams cutting back into the peat. Bilberry colonises the tops of the peat haggs as they dry out. Fairsnape Fell, Lancs.

large part of the "moorland" of the northern, north-western, and western Highlands is dominated by deer sedge. This community contains most of the species already mentioned, but it is on the whole a drier community than the Rhynchosporetum or Schoenetum of western Ireland and may contain such plants as tormentil (*Potentilla erecta*) and milkwort (*Polygala*).

The cotton-grass "mosses" are characteristic of the summit plateaux of the southern Pennines and occupy wide stretches of dreary monotonous moorland in which the tufted cotton-grass (*Eriophorum vaginatum*) is dominant alone (Phot. 93), sometimes with very few accompanying species. These Eriophoreta are about equivalent to the Highland Scirpeta and contain much the same species. Eriophoretum formed of the narrow-leaved species, *E. angustifolium*, is more characteristic of the northern Pennines.

Heather (*Calluna*) is present almost everywhere in blanket bog, as it is in raised bog, except in the wettest places, but it is never luxuriant and is often represented only by isolated and rather stunted plants. On the Highland moors, however, it is not infrequently co-dominant with deer sedge, and this degree of dryness of the peat in which heather and deer sedge are co-dominant may be taken to represent the dividing line between heath and bog. With further increase in dryness such as results from draining, heather becomes overwhelmingly dominant.

Hummock formation, which we saw to be the essential feature in the development of raised bog, is only local in the Irish blanket bog. Here and there isolated hummocks or groups of hummocks are formed by the activity of the bog mosses, the same species as in raised bog, and sometimes by the shaggy mountain moss *Rhachomitrium lanuginosum*, which, together with the silvery moss *Leucobryum glaucum*, very often caps the relatively dry tops of the hummocks (Phots. 91, 92). *Molinia, Calluna*, and sometimes *Erica cinerea* also freely colonise the surface of hummocks.

The succession of plant communities in blanket bog has not been properly worked out, but we may infer that the course of events is somewhat as follows. Blanket bog may originate either in pools of water or on wet soil, where the

reaction is markedly acid and the climate is wet enough. The moorland pools contain two characteristic species—bog bean (*Menyanthes trifoliata*, Phot. 91) and the pond-weed *Potamogeton polygonifolius*, and both of these may be found as relict species in the wettest places of the blanket bog, which mark the sites of former pools. The lakelets which are so common in the Connemara bogs are sometimes partly fringed with a sparse reedswamp of common reed (*Phragmites*) and saw sedge (*Cladium mariscus*), and these also may be found as relicts in the bog. When the pool or the lake margin has filled up with peaty humus so as to reach the water level, the surface is colonised by the alga *Zygogonium* (p. 189) and *Sphagnum cuspidatum*, then by *Rhynchospora* and its associates, and later by the other bog plants, with *Molinia* and *Calluna*, peat being steadily formed all the time.

Other successional phenomena are seen in the so-called "retrogression" of blanket bog which has been particularly studied on the cotton-grass "mosses" of the southern Pennines. This process depends essentially on drying of the peat as the result of erosion, either by wind or by the cutting back of stream channels into the peat plateau, and is greatly accelerated by fires which sweep over parts of the moss in the dry seasons. Round the head of a little stream valley which is being cut back into the plateau crowberry (*Empetrum nigrum*) appears and covers the eroded and drying peat slope. Cloudberry (*Rubus chamaemorus*) is also often found here. New tributary streams, draining the main mass of wet plateau peat, are established, and these also cut back into the plateau. Tributary channels from different systems eventually intersect as they increase in length by cutting farther and farther back, and thus isolated areas of peat, drained on all sides, are cut off (Phot. 94). The surfaces of such areas rapidly dry out and become unfavourable for the growth of the cotton-grass. They are then frequently colonised by bilberry (*Vaccinium myrtillus*), and sometimes by heather. Thus the original cotton-grass "moss" is destroyed and bilberry or heather "moor" takes its place. If erosion continues, the whole of the peat may be washed away and the underlying mineral soil exposed.

CHAPTER XII

MOUNTAIN VEGETATION

THE highest hills in the south-east of England scarcely reach 1000 feet, and this altitude at this latitude has no perceptible effect on the vegetation except that the rainfall tends to be higher and thus to encourage peat formation on the flat summits of hills composed of acidic rocks such as sandstones (for example, the summit of Hindhead), and that the strength of the wind on exposed slopes and summits tends to stunt the growth of woody plants. In the south-west there is a good deal of land lying above 1000 feet and there are summits of 1500 feet or more, just reaching 2000 feet on Dartmoor. The greater rainfall and the damper air of the south-western climate, enhanced at these relatively high altitudes, leads to the formation of wet moorland and blanket bog on the higher Dartmoor plateaux, but there are no specifically high-level ("alpine") plants or vegetation.

The hills of the north of England are higher, but except in the Lake District there are no summits of over 3000 feet, though in the northern Pennines there are a good many exceeding 2000, Cross Fell, the highest, reaching 2930 feet. Cheviot has a summit or two of over 2000 feet, and the Southern Uplands of Scotland have many. The highest slopes of these northern hills are grassland or moorland, with blanket bog on many of the plateaux and gentler slopes where the underlying rock is not easily permeable to water. On and around a few of the higher summits there are a small number of mountain plants, but very little in the way of specifically mountain plant communities. The same is true of most of Wales, except for Cader Idris in Merionethshire and especially Snowdonia, where there are several summits exceeding 3000 feet and many "arctic-alpine" plants are found. In Ireland, though several summits exceed 3000 feet, the mountain flora is poor, comprising fewer species than in Great Britain; and several of those which do occur are extremely rare. Some indeed

disappear before the summits of the mountains are reached. A striking feature is the number of "alpines" which descend to sea level on the west coasts, both of Ireland and Scotland, where they are often more abundant than on the mountains.

The higher mountains of the English Lake District, several of which exceed 3000 feet, possess more high-level species and small communities, and in North Wales, especially round Snowdon and the Glyders—of similar height—some of them are well developed; but it is only in the Scottish Highlands, where there are considerable areas and many summits over 3000 feet, while a few exceed 4000, that high-mountain vegetation is at all extensive, and even there only on certain mountains and mountain complexes.

The British plants which are confined or nearly confined to the higher mountains have been called "Highland" species, but they are now generally known as "arctic-alpine" species and the communities which they form as "arctic-alpine" vegetation. This is an appropriate name, for they are all plants whose main homes are either the arctic regions or the high mountain ranges of Europe such as the Alps, and often both. Species which are found at sea level in the Arctic are rarely found below 2000 feet in Britain (except on the west coasts) and do not occur much below 8000 feet in Switzerland. They are in fact the remains of the vegetation of the last ice age, and with the coming of a warmer climate, they have taken refuge in the far north and in the mountains, where the characteristic climate to which they are adapted, with its heavy snowfall, long duration of snow-lie, and correspondingly short growing season, still prevails. This is the central feature of the arctic-alpine climate as it affects the plants that live in it, and their habit and mode of growth are closely adjusted to these conditions. Trees and shrubs of normal stature are absent. There is an abundance of dwarf woody plants (technically called *chamaephytes* from the Greek χάμαι, meaning "on the ground"), not rising above 10 inches from the surface of the soil. At 2000 feet in the eastern Highlands the percentage of these dwarf shrubs in the total number of species present is twice as great as in the lowlands, and above 3000 feet nearly four times as great. At this altitude the chamaephytes make up a

quarter of the total flora; while more than one-half the total flora are perennials whose persistent buds which survive the winter actually lie upon or are embedded in the surface of the soil—*hemicryptophytes* (half-buried plants) as they are called.

Now plants belonging to these two "life forms" are covered with snow at the higher altitudes during most of the autumn and the whole winter and spring in a normal year. Thus on the top of Ben Nevis (4406 feet) the first snow appears in September, begins to lie in October, and the depth continually increases till May, when it begins to melt and evaporate, only disappearing in July, so that the growing season is confined to little more than two months. At somewhat lower altitudes, say 2500 to 3500 feet, where the arctic-alpine flora is most richly developed, the snow does not lie quite so long, but the growing season never exceeds three or four months. Snow is a bad conductor of heat, so that the plants are maintained during the winter at a temperature close to the freezing point and are not exposed to severe changes of temperature caused by alternate frosts and thaws as in the lowlands. When the snow disappears in the summer the soil warms up rapidly, especially on south-facing slopes, and the leaf and flower buds quickly open and take advantage of the short growing season. The low stature of the plants and the closely tufted habit which is common among them also give protection to their leafy shoots from the severe winds of these altitudes after the snow cover is removed. Exposed ridges and slopes where the wind constantly prevents snow from lying so that plants would be exposed during the whole year are commonly quite bare of vegetation.

In addition to long snow-lie and severe wind, the most important factors of the high-mountain climate as contrasted with that of the lowlands are the much lower average temperatures, and the rapid changes of temperature and of air humidity during the snow-free period. An outstanding feature of arctic-alpine vegetation is the prominence of mosses, and especially of lichens, most of which are very resistant to such conditions. A very large number of species of these groups occur in the arctic-alpine zone and many are confined to it, but particularly

striking is their massive conspicuousness in the vegetation. Everywhere at the higher altitudes they are locally dominant, and some dominate considerable communities such as the "*Rhachomitrium* heath" on exposed summits and plateaux (see p. 199). A moss and lichen vegetation similar to that of the higher English and Scottish mountains descends to and covers the summits of quite low hills in northern Scandinavia, and eventually, in the extreme north, it comes down to sea level as the widespread moss and lichen "tundra" of the "High Arctic."

Owing to the great diversity of high-mountain topography—the alternation of cliff, ledge, sheltered cleft or gully, scree, and rock-strewn plateau—there is a very wide variety of local habitat open to mountain plants, and a corresponding diversity of small plant communities. While the conditions of plant life are very hard in some of these habitats and the plants are sparse and stunted, in others they are very favourable, particularly where there is adequate shelter from wind and a good water supply. Here we find numerous lowland plants accompanying the arctic-alpine species, and often showing luxuriant growth, though many do not flower. These must have been transported by seed from lowland habitats.

If we take a general view of mountain vegetation as seen in the Scottish Highlands we must draw a broad distinction between the hills composed of hard intractable "acidic" rocks such as grits, slates, and some schists, and the more easily weatherable rocks, pulverising to fine mineral soil, such as certain other schists and some volcanic rocks containing abundant bases—particularly calcium and to a less extent magnesium and potassium. On the acidic rocks, of which most of the Scottish mountains are composed, subalpine moorland dominated by bilberry, sometimes with heather, and forming acid peat, extends up to a high level. To take a particular example, this bilberry community covers the Clova-Canlochan plateau in the eastern Grampians, on the borders of Forfarshire and Aberdeenshire, at about 3000 feet. The flora is poor and typical of such peaty moorland, with only a few arctic species such as dwarf birch (*Betula nana*), dwarf cornel (*Cornus suecica*), and arctic azalea (*Loiseleuria procumbens*)—all peat plants. On

exposed summits, where the drainage is good and peat cannot form, a few others may be found, such as the prostrate mountain cudweed (*Gnaphalium supinum*), alpine lady's mantle (*Alchemilla alpina*), with five leaflets spread out like the fingers of a hand (Phot. 99), the undersides covered with white hairs, and a mountain sedge (*Carex rigida*), the two last very widespread mountain plants. Actually the Clova mountains are very rich in arctic-alpine species, but the great majority are found only in the corries and by stream-sides in the high valleys, where the soil contains basic salts.

The Breadalbane Mountains in the Perthshire Highlands are largely composed of basic schists, and here the arctic-alpine flora and the development of arctic-alpine communities are also very rich. Ben Lawers (3984 feet), rising from the northern shore of Loch Tay, is the best known mountain of this type. After passing through the enclosed pastures near the lake one ascends over mat-grass (*Nardus*) moor up to about 2000 feet and then comes to higher boulder-strewn slopes covered with mountain grassland (Phot. 95). This is the first arctic-alpine vegetation encountered, and is a mixed community containing a large number of lowland species. The type of habitat is very favourable, especially when, as here, it is developed on a southern slope irrigated by numerous springs whose waters trickle through the boulders, bringing a good supply of basic salts. The bright green colour of the vegetation at once distinguishes this grassland from the dingy brownish-green mat-grass moorland of the peaty acid soils we have left behind, and it has much in common with limestone grassland. Sheep's fescue is the most abundant grass, and the "viviparous" form is common. In this form of the grass vegetative buds, each bearing a bunch of short bristle-shaped leaves, take the place of flowers, eventually becoming detached and rooting in the soil, thus propagating the plant. This "viviparous" habit is found among many alpine plants and is useful when the short growing season prevents the setting of seed. Other lowland grasses are freely mixed with the fescue. On Ben Lawers and many other Scottish mountains the alpine lady's mantle (*Alchemilla alpina*) is very abundant and conspicuous in this community, and a dozen or so other

arctic-alpine plants, in addition to the numerous lowland species, have been recorded from it. Similar high-level grassland, often dominated by sheep's fescue, occurs on most high mountains where the conditions are favourable, and it is not uncommonly used as sheep pasture in the late summer.

On a mountain of the height of Ben Lawers the continuous slopes are left behind when one climbs above the grassland, and at about the level of 3000 feet the mountain mass begins to break up into distinct summits separated by corries and high valleys and connected by cols and saddles. This is the zone inhabited by the richest and most varied mountain vegetation consisting mainly of arctic-alpine species, few lowland forms being able to exist except in the best protected and most favourable habitats.

The flat summits and gentler slopes exposed to the full force of the weather are typically covered by masses of boulders, slabs, or angular fragments split off from the parent rock by the action of frost, and often accumulated to a great depth. This is called by geologists "mountain-top detritus." When the stones are detached from the face of steep crags or vertical cliffs they fall, of course, on to the slope below and accumulate as "talus," forming the screes always seen below mountain crags. This is the most extensive high-mountain habitat and at the same time the poorest in species of higher plants.

The surfaces of the rock fragments and boulders forming the scree or the detritus of the plateaux are first of all covered by crust-forming lichens and by xerophilous [1] mosses, the latter spreading and beginning to bridge the gaps between the stones. Thus humus is formed and is washed down into the pockets and cracks of the stony mass so that they become filled with this humus, mixed with fine mineral soil worn from the rocks, in which higher plants can settle. In this way there is produced an open plant community composed of lichens, mosses, and a few scattered flowering plants. The habitat is naturally well drained and therefore the substratum is often very dry, but in wet and misty weather the surface is kept moist by the high humidity of the air. The plants are often completely

[1] Adapted to a dry habitat.

exposed to wind, which is frequently very violent, and also to extremes of temperature, though the severe winter frosts are much mitigated by the thick carpet of snow. The lower plants greatly preponderate both in bulk of vegetation and in number of species. No less than 172 species of lichen, 70 mosses, and 89 liverworts have been recorded from this habitat, the majority widely distributed species found also in the lowlands, but a considerable number confined to mountain habitats. The woolly fringe moss (*Rhachomitrium lanuginosum*) is one of the most abundant and conspicuous species.

The higher plants are much fewer and the great majority of them are arctic-alpine species, most of which have a characteristic cushion or mat-forming habit that affords considerable protection through the low stature and close setting of the shoots. Thus the "stemless" campion (*Silene acaulis*) has flowers seated in a thick cushion of closely packed shoots, the alpine azalea (*Loiseleuria procumbens*) and the large purplish-flowered saxifrage (*Saxifraga oppositifolia*) form surface mats of intertwined branches. A mountain woodrush (*Luzula spicata*) and the commonest sedge of this habitat (*Carex rigida*) have mats of intertwined rhizomes and shoots just below the soil surface, while the rhizomes of the little herbaceous willow (*Salix herbacea*) are more deeply buried. The lowland species are very restricted in number and either have a similar mat-forming habit, as in crowberry (*Empetrum nigrum*) and bilberry (*Vaccinium myrtillus*), or are much stunted in growth, as in mat-grass, wavy hair-grass, and goldenrod (*Solidago virgaurea*). Most of the species propagate vegetatively and several are viviparous. There is great wastage of higher plant life under these conditions. It is constantly recruited from more favourable habitats, but most of the immigrants do not survive. When the exposed detritus is immediately adjacent to rock ledges and corries with a rich flora the number of species is considerably increased.

Under slightly less exposed conditions the woolly fringe-moss (*Rhachomitrium lanuginosum*) increases and becomes definitely dominant, covering the boulders with continuous growth, and at the same time forming an extensive bed of raw humus in which such heath plants as are able to

tolerate the conditions of exposure can establish themselves. The mosses and lichens are here greatly reduced in number of species owing to the overwhelming competition of the thick massive fringe moss. Among flowering plants the heath family are conspicuous, including bearberry (*Arctostaphylos uva ursi*), alpine bearberry (*Arctous alpina*), heather (*Calluna*), dwarf bilberry (*Vaccinium myrtillus*), cowberry (*V. vitis idaea*), and the arctic-alpine *Vaccinium uliginosum*. Dwarf crowberry (*Empetrum nigrum*), of similar habit and requirements, also occurs. Other plants of peaty soil are the two arctic-alpine clubmosses (*Lycopodium selago* and *L. alpinum*), dwarf cornel (*Cornus suecica*), and the dwarf willow *Salix herbacea*. A few stray lowland plants are tolerant of these conditions, such as harebell (*Campanula rotundifolia*), tormentil (*Potentilla erecta*), heath bedstraw (*Galium saxatile*), and sorrel (*Rumex acetosa*). Wavy hair-grass and sheep's fescue may also occur. This community is often known as "*Rhachomitrium* heath" because of the dominance of the woolly fringe moss and the prevalence of heath plants.

On stable screes, i.e. those on which the supply of falling stones has ceased owing to the wearing down of the crags above, substantially the same plant communities occur, i.e. both the open community dominated by mosses and lichens and the *Rhachomitrium* heath. Very old screes or detritus at a somewhat lower altitude, where they are formed of rocks weathering to a fertile soil and well irrigated, develop, as we have seen, a much richer community of grassland type and with a preponderance of lowland species.

Screes, of course, often occur well below the arctic-alpine zone, in fact at any altitude where a flat or gently sloping terrain is overhung by weathering crags. Here the amount and nature of the vegetation able to colonise the scree depends upon the altitude and also upon the nature of the stones and their mobility. On a very mobile scree the vegetation is at a minimum, but on non-calcareous screes, different parts of which show different degrees of mobility, the less mobile stones are colonised by rock lichens, and the interstices between them, in which fine soil has been collected, largely by a liverwort (*Diplophyllum*) and by

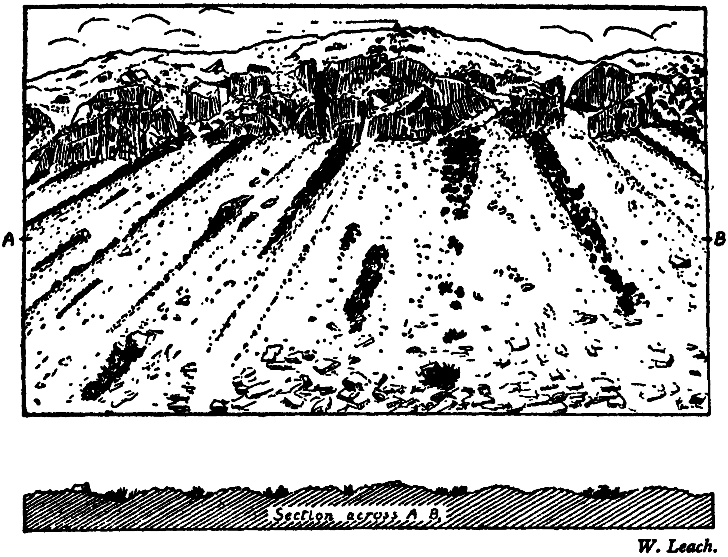


FIG. 5. Development of vertical strips of vegetation on screes.

Rhachomitrium. In the cushions formed by these plants the parsley fern (*Cryptogramma crispa*) settles down and forms quite large plants after a number of years. In the humus accumulated by the fern other plants germinate, such as the bents, sweet vernal grass, wavy hair-grass, sheep's fescue, heath bedstraw, etc., and a large number of mosses. This vegetation is always liable to be destroyed by a renewal of the activity of the scree, but if sufficient stability is maintained heath plants arrive, including bilberry (which often invades by rhizome growth from the edge of the scree), purple bell-heather, cross-leaved heath, and ling (*Calluna*). This heath vegetation is frequently developed in vertical strips (Fig. 5 and Phot. 18, p. 98), stretching down the scree from quiescent points, either below portions of crag from which stones are not falling continuously, or, farther down the scree, below large fallen blocks which hold up the downward movement of talus, and thus ensure at least temporary stability to the vertical strips below. If the whole scree becomes stable it eventually becomes covered by heath dominated by bilberry or heather. Below about 1500 feet the heath may be colonised by oaks if seed parents are available, so that dwarf

woodland develops (Phot. 18, p. 98). On stable calcareous screes at similar altitudes ashwood develops in an analogous way (Phot. 40, p. 118).

Comparative study of the vegetation of mountain-top detritus and scree at various altitudes illustrates the principle of succession and its arrest by various factors. The initial colonisation of this type of habitat by lichens and mosses, the accumulation of humus by dead plant substance and of mineral soil by weathering of the talus, the invasion of heath plants and formation of a continuous vegetative cover, and the eventual arrival of trees to form woodland, is the normal prisere or complete succession (see p. 62). But at high altitudes with extreme exposure and also on moderately mobile scree the sere never progresses beyond the first stage. With slightly better protection and on quiescent scree the second stage is reached, and within the climatic limit of woodland the third and final phase can develop.

To return to the ascent of a mountain like Ben Lawers. When the grasslands have been left behind at about 3000 feet and the cliffs, ledges, and corries between the high summits are reached, we enter a region of great physiographical diversity and correspondingly small habitats and small plant communities. These are not dominated by single species, but consist of a great mixture. Often the habitat is so broken up, conditions varying within a few feet or even a few inches, that we cannot properly speak of "communities" at all. On the ledges and in the nooks and crannies of this region numerous arctic-alpine species, including most of the rarest, are found. A common character of these habitats is the relative protection they enjoy.

The bare rock faces are occupied by certain algae and by very numerous species of lichen, of which more than a third are arctic-alpine forms. The majority belong to a few genera (*Aspicilia*, *Gyrophora*, *Lecanora*, *Lecidea*, *Rhizocarpon*) specially adapted for colonising naked rock, and they are accompanied by a much smaller number of rock mosses, largely belonging to the genera *Andreaea* and *Grimmia*. On slightly eroded rocks other species come in, and on moist rock surfaces liverworts increase in numbers where algae

A. G. T.

PHOT. 95. Arctic-alpine grassland at 2700 ft. on Ben Lawers. Alpine form of the sheep's fescue (*F. ovina* forma *vivipara*) and alpine lady's mantle (*Alchemilla alpina*). Lichen-covered boulders.

F. F. Laidlaw

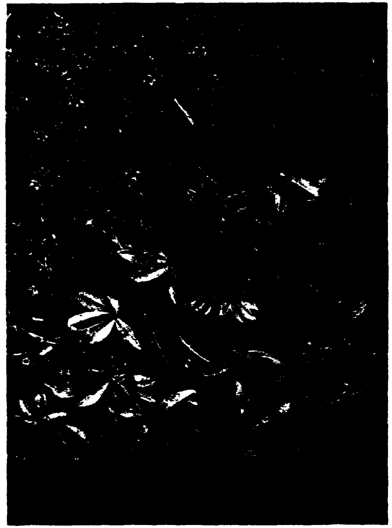
PHOT. 96. Alpine fleabane (*Erigeron alpinus*), a very rare arctic-alpine plant, and sheep's fescue, on a steep open ledge on Ben Lawers at 3500 ft.

J. Massart

PHOT. 97. Rose root (*Sedum rhodiola*) and alpine lady's mantle (*Alchemilla alpina*) on steep rocks at 3600 ft.

N. F. G. Cruttwell

PHOT. 98. Ferns in a rock cleft: *Athyrium alpestre*, *Cystopteris fragilis*. *Polystichum lonchitis*. On the side *Oxyria digyna* above; *Alchemilla alpina*.



J. Massart

PHOT. 99. Alpine lady's mantle (*Alchemilla alpina*) and Cyphel (*Minuartia sedoides*).

or lichens have already provided a film of organic substance. Owing to the rapid erosion of the more friable rocks due to water, frost, changes of temperature, wind, and the action of the lower plants, pockets of mineral soil soon collect and piles of fine soil mixed with rock fragments may often be found even on level surfaces where they are protected from wind, while gaps and fissures are soon partly or wholly filled with similar material.

Higher plants cannot, of course, colonise bare rock faces, because they must have some kind of soil in which to root, but a number settle on ledges with a very thin soil layer. These are nearly all arctic-alpine plants and include some of the species already recorded from mountain-top detritus, such as stemless campion and opposite-leaved saxifrage, together with several other species of saxifrage with white flowers (*Saxifraga cernua, hypnoides*, and *nivalis*), the beautiful roseroot (*Sedum rosea* or *rhodiola*), alpine lady's mantle (Phot. 97), *Erigeron alpinus* (Phot. 96), and many others, including ferns such as the green spleenwort (*Asplenium viride*) and the rare *Woodsia alpina*. A very few lowland plants such as harebell and thyme may be found in this habitat.

Where there is abundance of soil and good shelter a variety of other species is met with, many mosses, liverworts, and a few lichens, with vascular plants. The majority of species here are lowland plants, though there are several distinctive arctic-alpines too. The community is often nearly closed and the growth luxuriant because of the favourable conditions. Among the lowland species are common angelica (*Angelica silvestris*), broad buckler fern (*Dryopteris dilatata*), the large red-flowered cranesbill (*Geranium silvaticum*), the great woodrush (*Luzula maxima*), common red campion (*Melandrium dioicum*), spotted orchis (*Orchis maculata*), wintergreens (*Pirola*), stone bramble (*Rubus saxatilis*), sorrel (*Rumex acetosa*), and globe-flower (*Trollius*).

Some of these habitats with deep soil are heavily shaded, as in wide and deep rock fissures or in deep hollows among block screes. Here both soil and air are kept moist and the conditions are very favourable for woodland plants, unless indeed the light is so feeble that the plants become weak

and very pale. Among the lowland woodland plants that may occur in such situations are moschatel (*Adoxa moschatellina*), wood anemone (*Anemone nemorosa*), wavy bitter-cress (*Cardamine flexuosa*), herb-robert (*Geranium robertianum*), and woodsorrel (*Oxalis acetosella*). It is something of a shock when one first meets these familiar lowland plants at over 3000 feet among the arctic-alpine flora composed of such species as holly fern (*Polystichum lonchitis*), alpine lady-fern (*Athyrium alpestre*, Phot. 98), alpine sedges and woodrushes, arctic willows and saxifrages. Mosses and liverworts are fairly numerous in this habitat and include some arctic-alpine forms. There are a few lichens but they are not characteristic of the habitat, which is too dark for most of them.

Wet habitats are common and varied on many of the higher mountains, including Ben Lawers. Springs emerge at quite high altitudes and form numerous small shallow runlets which ultimately converge to form the "burns" (Scotland) or "becks" (north of England) which run down the mountain-side at lower levels. On the schistose mountains the alternation of harder and softer layers of rock leads to the formation of series of terraces, and the excess water from the springs and runlets flows gently over these and percolates among the detached boulders. The soil of this habitat on Ben Lawers consists of flakes and fragments of mica-schist caught among the larger boulders. Irrigated by the moving spring water, well aerated, and abundantly supplied with nutrient salts, it forms a well-marked and very favourable habitat for vegetation—a wet bright green carpet of mosses, liverworts, and algae, with a smaller number of flowering plants.

Several moss and liverwort societies can be distinguished here, the commonest and most conspicuous dominated by the moss *Philonotis fontana*, which forms most of the typical bright green carpet referred to. Other societies are dominated by liverworts, two of these (*Scapania obliqua* and *Sphenolobus politus*) being arctic-alpine species. A considerable number of other mosses and liverworts occur in this general habitat, a proportion of both being arctic-alpine species. Of the mosses, *Aulacomnium palustre*, growing gregariously in cushions, like *Philonotis*, is frequent, and

so are many species of *Hypnum*: among liverworts species of *Aplozia, Marzupella, Scapania*, etc. Species of *Sphagnum* are not characteristic, because the fresh spring water with abundance of basic mineral salts is at the opposite pole from the acid peat bogs which are their typical habitat, but certain species such as *S. inundatum* and *S. cymbifolium*, which tolerate alkalinity, may be found in places.

The flowering plants include an almost equal number of arctic-alpine and lowland forms. Among the former are mountain species of sedge (*Carex saxatilis* and *vaginata*), dwarf rushes (*Juncus biglumis* and *triglumis*), alpine willowherbs (*Epilobium alsinifolium* and *anagallidifolium*), saxifrages (the white-flowered *Saxifraga stellaris* and the yellow-flowered *S. aizoides*), alpine mouse-ear chickweeds (*Cerastium alpinum* and *cerastioides*), hairy stonecrop (*Sedum villosum*), mountain sorrel (*Oxyria digyna*, Phot. 98) —a widely spread mountain plant not confined to the wettest places—alpine meadow-rue (*Thalictrum alpinum*) and alpine veronica (*Veronica alpina*). Of lowland species there are the small mountain variety of marsh marigold (*Caltha palustris* var. *minor*), various forms of the common lady's mantle (*Alchemilla vulgaris*), the golden saxifrages (*Chrysosplenium*), forms of scurvywort (*Cochlearia*), the little waterblinks (*Montia fontana*), butterwort (*Pinguicula vulgaris*), various sedges (*Carex*), etc.

The high-mountain flora of Great Britain does not yield such glorious sheets of colour as the alpine pastures of Switzerland, because there are no such great stretches of grassland suitable for pasture at a high altitude, and the summers are on the average much cooler and wetter, so that there is no possibility of a seasonal pastoral industry within the arctic-alpine zone. Though the number of alpine species is not nearly so great as in the Alps, the Pyrenees, or the Carpathians, it is not inconsiderable—between one and two hundred flowering plants—while many of the plants are very attractive and some of the flowers strikingly beautiful. Fortunately our high-mountain vegetation is fairly safe from destruction—except by the ravages of selfish collectors—because man has not yet found a way of utilising the higher mountains for material purposes.

CHAPTER XIII

FRESHWATER VEGETATION

PLANTS which live submerged or partly submerged in permanent bodies of water (aquatic plants), or with their roots in permanently wet soil (marsh and fen plants), are never subject to drought as ordinary land plants may be. On the other hand, submerged plants are dependent for oxygen on what is dissolved in the water. Moving waters, especially rapidly-flowing streams, contain plenty of dissolved oxygen, but in stagnant waters there may be a severe shortage, in contrast with the unlimited supply from the air available to land plants. Plants which float freely below or on the surface, or which are simply attached to rocks or to other plants, have to get all their mineral food from what is dissolved in the water, but those which are rooted in the mud or sand at the bottom of a pond or river get most of theirs by absorption from this subaquatic soil, just as land plants get it from subaerial soil.

Rivers, lakes, and pools therefore contain very different vegetation according to their rate of flow or stagnancy, and according to the amount and composition of the *silt* covering their floors. Mountain tarns, lakes lying in basins composed of hard insoluble rocks, and rivers flowing over such rocks, accumulate little or no silt on their beds and correspondingly support a sparse vegetation or almost none: the plants which do grow in them belong to species that can manage with a poor and scanty soil. At the other extreme rivers flowing over soft rocks easily eroded by the current remove much material from their banks and bed in times of flood, and this is ultimately deposited as silt when the current slackens its pace. In this way silt accumulates on the bed and a rich aquatic vegetation is developed. Fans of silt are also deposited round the mouths of rivers and streams entering a lake, and are colonised by aquatic plants. When the silt rises above the surface a delta is formed and marsh vegetation supersedes the aquatic. Silt is often carried by currents along the shores of a lake and similarly

colonised when it comes to rest. If a river drains manured agricultural land the silt is greatly enriched by organic material washed into the water and the aquatic vegetation is particularly luxuriant. The same is true of ponds into which rain-wash is carried from surrounding manured land. Only if there is a great excess of organic material does the water become foul and ordinary plant-growth is very poor or absent. This can be seen in small ponds heavily fouled by cattle, and in ponds and sluggish narrow streams overhung by thick bushes where the water is filled with dead and decayed leaves.

Freshwater plants show a great variety of life forms. The primitive water plants belong to the great class of *Algae*. These lower, primarily aquatic plants, include not only the marine "seaweeds," often bulky and of fairly complex structure, but numerous very minute or delicate, mostly green, freshwater forms, either unicellular or consisting of simple threads of cells. There are also a number of aquatic mosses and liverworts, and many flowering plants belonging to various families. Unlike the *algae* the more or less remote ancestors of all the aquatic *flowering* plants originally lived on land, and some of their descendants have become modified for life in water.

The most profoundly adapted of British flowering water plants are those whose vegetative bodies are completely submerged in water, such as Canadian waterweed (*Elodea*), several pondweeds (*Potamogeton*), and many others. Their leaves are either entire, often thread-like or band-shaped and very thin, or "dissected," i.e. divided into slender thread-like branches. All the living cells of the leaves of such plants are thus very close to the surrounding water, from which they absorb dissolved gases (oxygen and carbon dioxide) and mineral substances, so that they do not require much in the way of conducting tissues. Both the band-shaped and the thread-shaped types of leaf offer the least possible resistance to the current of a river, the leaves streaming out with the flow of water, as can easily be seen by looking over the parapet of a bridge at the submerged plants growing on the bed of a clear stream.

Many water plants, e.g. water plantain (*Alisma plantago-*

aquatica), arrowhead (*Sagittaria sagittifolia*, Phot. 100), and some of the white-flowered water crowfoots or water buttercups (*Ranunculus*, section *Batrachium*) have their lower leaves submerged (band-shaped or finely divided) and their upper leaves, of different shape, displayed in the air above. Others again have leaves floating on the surface of the water (Phots. 103, 104, 105), as in the water lilies and some of the pondweeds (*Potamogeton*). Most bear their flowers above the surface of the water.

Generally the submerged plants occupy the deepest water, while the shallower parts are occupied by the forms with floating leaves or partly emersed shoots. Towards the edge of the water we have the plants of the "reedswamp" with tall shoots rising several feet above the surface of the water and most or all of the leaves aerial. The most widespread of these are the common reed (*Phragmites*), which is a grass; reedmace or bulrush (*Typha*, Phot. 111); and the lake reed, also called "bulrush" (*Scirpus lacustris*, Phot. 103), with long, slender, cylindrical, dark green leaves much like the stems. There are many other reedswamp plants, including several of the large sedges (*Carex*) and bur-reed (*Sparganium*, Phot. 106), hairy willowherb (*Epilobium hirsutum*), yellow loosestrife (*Lysimachia vulgaris*), red loosestrife (*Lythrum salicaria*), etc., etc.

Thus in a pond or slow river there is well-marked *zonation* of the vegetation. In the middle of a good-sized and fairly deep pond the surface of the water will be unbroken by vegetation, but there may be a rich growth of completely submerged plants floating freely or growing on the bottom. Nearer the edge, in shallower water, come plants with leaves floating on the surface, and others with leaves and inflorescences emerging above the surface, while the margin of the pond is often occupied by a dense reedswamp which may extend to the flat wet soil beyond the edge of the water. A good example of this is shown in Figs. 6 and 7. The different zones are not always sharply divided but often overlap, so that plants of two or more life forms may occur together. For example, the loose outer edge of reedswamp, away from the margin of the pond or lake, may have a lower storey of water lilies, whose floating leaves occupy the spaces between the sparse

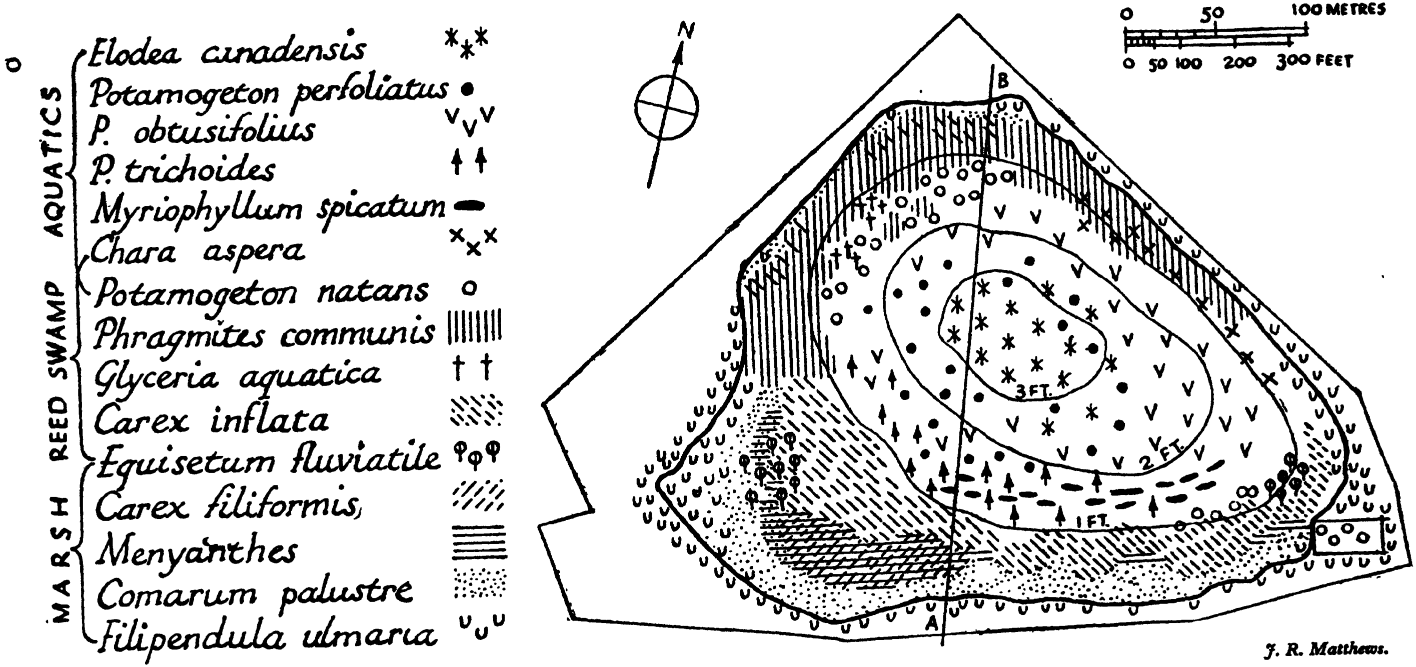


FIG. 6. Plan of White Moss Loch, Perthshire, showing zonation of aquatic, reedswamp and marsh vegetation.

ascending shoots of the reeds and thus get protection from wave action.

The zonation of vegetation in a pond or on the silted edge of a lake is often an expression of *succession.* This depends upon the gradual shallowing or "filling up" of the water by the accumulation of silt or of the dead and partly decayed remains of the plants (subaquatic humus) or by both processes together. When the water has become shallower the completely submerged plants are crowded out and superseded by those with floating leaves or partly emersed shoots, and these, in their turn, as the water

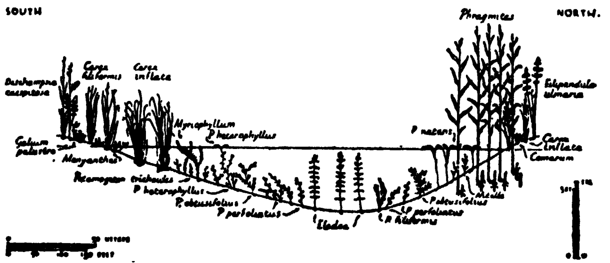


FIG. 7. Profile of vegetation of White Moss Loch, Perthshire.

becomes still shallower, by plants of the reedswamp. In this way a small pond often becomes completely filled up with reedswamp if it is not cleared out at frequent intervals.

The successional process does not stop short at that. The accumulation of dead plant material continues after the soil level has reached the surface of the water, and the reedswamp is then invaded by marsh and fen vegetation. This will be considered in the next chapter. Reedswamp is the ultimate term of the *aquatic* succession, and in its turn leads on to marsh and fen, thus forming a transition from water to land vegetation.

The majority of small ponds in cultivated land are artificial, commonly dug for watering cattle. Many are also formed in old pits from which sand or gravel or brick earth or soil for ballast has been removed, and into which water has drained. Recently dug ponds which are only in early stages of colonisation differ very much in their flora

R. H. Yapp

PHOT. 100. Arrowhead (*Sagittaria sagittifolia*) in aquarium: submerged leaves band-shaped.

J. Massart

PHOT. 101. Submerged leaves of arrowhead in the River Cam.

R. H. Yapp

PHOT. 102. Bladderwort (*Utricularia*) in aquarium. Finely cut leaves all submerged.

J. Massart

PHOT. 103. Floating leaves of yellow water lily and floating pondweed in the River Cam. Shoots of bulrush (*Scirpus lacustris*) behind.

R. H. Yapp

PHOT. 104. Yellow water lily (*Nuphar luteum*).

R. H. Yapp

PHOT. 105. White water lily (*Nymphaea alba*).

according to the varying chances which have brought the seeds or fruits or bits of water plants to the pond from other similar habitats. Many water plants easily reproduce themselves from broken fragments of the vegetative plant body.

The Canadian waterweed (*Elodea canadensis*), which was only introduced into England in the middle of last century, spread with remarkable rapidity and vigour, entirely by vegetative means, through our slow rivers, ponds, lakes, and canals, so that it became a pest. It is now much reduced in quantity though it is still a frequent constituent of our freshwater vegetation and is one of the commonest members of the entirely submerged aquatic community. Bladderwort (*Utricularia*) is a free-floating plant with finely dissected leaves and remarkable bladders in which it catches and digests tiny aquatic crustacea. Its inflorescences are displayed above the surface of the water (Phot. 102). Numerous species of pondweed (*Potamogeton*), some with filiform leaves (*P. pectinatus, P. pusillus*), others with ovate or elliptical leaves (*P. perfoliatus, P. densus*), are also common submerged species. Water milfoils (*Myriophyllum spicatum* and *alterniflorum*), growing in one to two feet of water, have most of their shoots submerged, the leaves divided into filiform branches, but the inflorescences above the surface of the water. Several of the water crowfoots (water buttercups), with white flowers, have all their leaves submerged and finely divided into narrow segments (*Ranunculus fluitans*, Phot. 107, *R. trichophyllus*, etc.). Others (*R. heterophyllus*) have in addition, expanded leaves which float or are held above the surface of the water.

The common rooted water plants with leaves which float on the surface of the water are pondweeds, *Potamogeton natans* and *P. heterophyllus* (which also has submerged leaves), and the yellow and white water lilies (*Nuphar luteum* and *Nymphaea alba*, Phots. 104, 105). Species of duckweed (*Lemna*) are minute free-floating plants specially common on the surface of small ponds. The whole plant is composed simply of a tiny floating plate or frond of green cells, with a single root descending a fraction of an inch into the water (*Lemna minor*, the commonest species), or

several such roots (*L. polyrhiza*), or none (*Wolffia arhiza*). Duckweeds grow most luxuriantly in ponds containing much organic matter in solution and reproduce themselves very vigorously by budding from the edges of the fronds: in this way they may rapidly spread over the entire surface of a small stagnant pond. Plants with floating leaves can only maintain themselves in quiet waters: surface wave action destroys them. Thus they are often found among the reedswamp plants on the edge of a lake where they get adequate protection. The characteristic reedswamp plants can withstand moderate wave action because their long flexible stems can bend before the waves. Shores on which waves beat violently are bare of vegetation.

We have seen that the great luxuriance of the vegetation of many lowland ponds and rivers depends upon the nature of the soil or silt in which they grow. Characteristic of the soils and silts rich in nutritive salts are Canadian waterweed (*Elodea*); many of the submerged pondweeds; water plantain (*Alisma*) and arrowhead (*Sagittaria*)—both plants with partly emersed leaves and inflorescences; the yellow and white water lilies (*Nuphar* and *Nymphaea*), with floating leaves; most of the reedswamp plants, especially reedmace (*Typha*) and to a somewhat less degree the common reed (*Phragmites*) and the lake reed or bulrush (*Scirpus lacustris*). But there are other aquatic plants which grow on substrata with a minimum of silt, as among the stones on the floors of certain lakes, or where the silt is of the nature of acid peat, poor in nutritive salts. Many of the lakes of the English Lake District have both these types of water plants on different parts of their shores.

It has been shown by Professor Pearsall, to whom we owe most of our knowledge of this subject, that the different lakes of this district form a series illustrating the evolution of glacial lake basins from a primitive type with rocky floor, stony or peaty margins, and little or no inorganic silt, to the richly silted substratum which is found on parts of the shores of the more advanced lakes, such as Esthwaite Water, into which streams bring abundant inorganic silt. This silt is, however, quite local in distribution, being confined to the delta-like fans formed

at the mouths of the streams and to certain other parts of the lake shore to which it is carried by currents.

One of the characteristic pioneers of the vegetation developed on stony lake bottoms, poor in silt, is the quillwort (*Isoetes lacustris*), a cryptogamic plant with a stem represented by a small corm and a rosette of long linear leaves. The *Isoetes* community normally grows on stones masked by a thin layer of silt, or on boulder-clay. Together with other deep-water communities it is only found where the light intensity is less than 15 per cent. of full daylight. In a clear lake this may be 4 metres down from the surface of the water, but in a heavily silted lake where the light does not penetrate so far the deep-water communities may reach to within one metre of the surface. Vegetation does not descend below the point at which the light intensity is reduced to 2 per cent. of full daylight, and sometimes not so far. In Wastwater, a very clear lake, reduction to 2 per cent. is found at a depth of 10 metres, while the vegetation only descends to 7·7 metres. In the well-silted and peaty waters of Esthwaite reduction to 2 per cent. of the light occurs at 4·1 metres and the vegetation descends to 4 metres.

Other dominant deep-water plants of these lakes are species of *Nitella*, belonging to the isolated group of "charads" or "stoneworts," so called because some of them which inhabit calcareous waters are thickly encrusted with lime. The charads resemble algae in many ways but are of more complex structure than the green freshwater algae, though very much simpler than vascular plants. The *Nitella* communities (*N. opaca* and *N. flexilis* dominant) are found in all the lakes and cover the most extensive areas on deep-water silts.

With *Nitella* are associated many species of fine-leaved, delicate pondweeds (*Potamogeton*), and some of these (e.g. *P. pusillus* var. *lacustris*) also form separate communities where there is abundant inorganic silt. In many places, too, there is a collection of species, no one being generally dominant, called by Pearsall the "linear-leaved associes," of strikingly uniform life form. "All have the pellucid linear leaves and delicate stems of the *Potamogeton pusillus* type." The complete list includes 7 species of pondweed

and 6 others—*Naias flexilis, Callitriche autumnalis* (water starwort), *Elodea canadensis* (Canadian waterweed), *Hydrilla verticillata, Myriophyllum alterniflorum* (water milfoil), and *Nitella flexilis.* All these, except *Nitella,* are flowering plants of very various affinities, showing the overwhelming effect of the specialised habitat in producing a similar life form.

The shallow-water communities of the Cumbrian lakes normally occur in light of more than 15 per cent. of full intensity. They are not necessarily developed in succession to deep-water communities, but also colonise eroded shores *de novo.*

A pioneer community on gravelly soils is the *Littorella-Lobelia* associes. *Littorella uniflora* ("shoreweed") colonises the loose gravel where there is no organic silt at a depth of 1 to 4 (sometimes 6) feet, and by means of its vegetative reproduction spreads over and stabilises the substratum. It then catches seeds of *Lobelia dortmanna* (a submerged plant with a loose scape of elegant lilac flowers rising above the water) which joins *Littorella* to form a closed community. As the soil becomes more organic the shoreweed dies out while other plants appear—milfoils (*Myriophyllum*) and *Juncus fluitans,* the last only where the soil is peaty with a highly organic content. Where the soil remains inorganic, with a high percentage of potash, *Littorella* is succeeded by species of pondweed (*Potamogeton gramineus, P. nitens,* etc.).

Following on these submerged shallow-water communities come the plants with floating leaves, the large-leaved pondweed (*Potamogeton natans*) succeeding *Myriophyllum* and *Juncus fluitans* where the organic content of the soil is high. Water lilies, especially the white water lily (*Nymphaea alba*), are found only where the organic content is quite low and there is abundant inorganic silt, as in Esthwaite Water.

Finally we come to the reedswamp plants, which again show a contrast between highly organic, peaty soils and those which contain abundant inorganic silt. On the former we have a species of horsetail (*Equisetum fluviatile*) with ungrooved stems [1] from 1 to 8 feet high, and, especially on

[1] Most of the horsetails are wet-soil land plants with grooved stems.

the most organic soils, certain species of tall sedge (*Carex inflata*, *C. vesicaria*, and less commonly *C. lasiocarpa*) dominant. This reedswamp is characteristic of the more rocky lakes where silting is at a minimum.

The commonest type of reedswamp occurs on sheltered lake shores where the soil is less organic and is dominated by the common lake-reed or bulrush (*Scirpus lacustris*) and the common reed—really a grass—(*Phragmites communis*), which are the two most widespread European dominants of reedswamp. They occur either mixed or in pure communities. *Scirpus* extends into the deeper water (to 1·3 metres) and also prefers the more organic soils: the flexibility of its stems withstands wave action better than does the common reed. *Phragmites* forms the bulk of the inshore reedswamp (to a depth of 0·92 metre), and also persists in the fen where the soil is raised above water level. In the Cumbrian lakes both are of restricted distribution because of the resistant nature of the substratum and its instability. They occur in open bays where wave action and silting are both slight, round the mouths of streams, and in extensive shallows. The dominants are usually so closely set that there is little room for other plants between them, but in the outer fringe where the reeds are only just establishing themselves a few other species occur.

The third tall reedswamp dominant is the great reedmace, very commonly called "bulrush," *Typha latifolia*. In the Lake District this is only found in one place, at the mouth of the Black Beck at the head of Esthwaite Water, where there is an exceptional abundance of fine silt brought down by the stream. In the English lowlands *Typha*, *Phragmites*, and *Scirpus* often occur together on the margins of ponds and lakes, and are commonly zoned in that order (as they are at Esthwaite), *Typha* being nearest the shore line and *Scirpus* the farthest out. Another species of *Typha*, *T. angustifolia*, the narrow-leaved bulrush, sometimes forms extensive reedswamps, as for instance at Heigham Sound in the Norfolk Broads.

In the smaller mountain tarns no great development of vegetation is possible. In some there is very little silt, what there is being inorganic and derived from erosion of

their shores. Here the vegetation is very scanty, the species of deep water being *Isoetes*, *Nitella*, and *Myriophyllum*, with a few others where some inorganic silt is deposited. In shallow water *Littorella* is the principal species. In small tarns where the shores are not eroded so that there is no inorganic silt, but peaty silt comes from the terrestrial peat formed in bog surrounding the lakelet, the substratum is organic, and there is a good succession from the aquatic communities to those of the adjacent bog. The vegetation begins in deeper water with *Juncus fluitans* and water milfoil (*Myriophyllum*) together with small bladderwort (*Utricularia minor*) and species of *Chara* and *Nitella*. This open community is followed by the entirely submerged small bur-reed (*Sparganium minimum*) and then by a floating-leaf community of small water lilies (*Nymphaea occidentalis* and *Nuphar pumilum*). Next comes the horsetail *Equisetum fluviatile*, and finally reedswamp of the tall sedge *Carex inflata*, with which are associated small bladderwort (*Utricularia minor*), bog bean (*Menyanthes trifoliata*), a characteristic species of pondweed (*Potamogeton polygonifolius*), and narrow-leaved cotton-grass (*Eriophorum angustifolium*). These last three species all occur in the wettest bogs (see Chapter XI), so that this marginal reedswamp forms a transition from the aquatic vegetation of the tarn to that of the surrounding bog. As the peaty soil reaches the water level, bog moss (*Sphagnum*) begins to appear, with cross-leaved heath (*Erica tetralix*) and the sedge *Carex panicea*, followed by other species of bog plants, till typical bog is established. Patches of bog bean and of *Potamogeton polygonifolius* in the bog often mark the sites of vanished lakelets which have become filled with peat.

This is an example of a continuous succession from water to land vegetation. In the larger Cumbrian lakes, however, there is usually a break between the strictly aquatic plant communities and the development of land vegetation. This is because the shores of these lakes are largely rocky, and over long stretches severely wave-beaten, so that there is a zone in which vegetation cannot maintain itself. As a result the aquatic series of plant communities forms a succession (or rather several successions) separate from

those of the land. It is only where the marginal zone is quiet and richly silted, or where the formation of peat is continuous throughout, that there is continuous succession from water to land communities, as in the tarns surrounded by bog just described and in lowland ponds on soft soil.

THE VEGETATION OF RIVERS

The continuous current of a river is, of course, the condition which differentiates it as a habitat from a pond or lake, and the swifter the stream the more marked is the difference. In rivers of very slow current (say less than five inches a second), such as the sluggish streams of the plains where the gradient is very slight, the vegetation approximates to that of the pond: in swift mountain torrents, where the average rate of flow is more than four feet a second, it is entirely different; and there are all gradations between these extremes.

A river with a long course, whose sources are in the mountains and which flows down through foothills to the plains, and thence to the sea or to its junction with a larger river, shows all these gradations successively. The silting factor is just as important as it is on the floors of lakes and for the same reason—that the more luxuriant flowering water plants depend upon the abundance and nature of the silt on the river-bed for establishment and good growth. Silt is brought down from the higher reaches where the river erodes its banks, and is also brought into the stream after heavy rain by floodwater from the adjacent land. It is deposited wherever the river current slackens to a certain degree, as at a sudden bend or decrease of gradient. River currents also change their velocity very considerably according to rainfall or the melting of snow along the upper reaches—sometimes within a few hours. When there has been heavy rain or quickly melting snow in the mountains a great rush of floodwater comes down the rivers, raising their level, eroding their banks, and sweeping away silt that had been previously deposited.

The beds of mountain torrents are rocky or covered with large boulders, and their vegetation is composed mainly of mosses and liverworts, which sometimes carpet the rocky

bed, together with a few lichens. Flowering plants are sparse or absent altogether because they can rarely get secure foothold and because of the absence of silt.

Rivers with a moderately swift current, round about 2 feet a second, and with a bed composed mainly of stones, have a vegetation still consisting largely of mosses and liverworts, but also of flowering plants rooted in the silt, which is here and there trapped in small quantities between the stones. These plants can maintain themselves only where the floods are not strong enough to tear them out. The common dominant of the communities of flowering plants in such situations is a species of water crowfoot *Ranunculus fluitans* (Phot. 106), together with submerged forms of "water parsnip" (*Sium erectum*), "water celery" (*Apium nodiflorum*), a species of pondweed (*Potamogeton densus*), and more rarely forget-me-not (*Myosotis scorpioides*), and a water speedwell (*Veronica anagallis-aquatica*). These plants grow in long streaks of varying width, their shoots trailing downstream and sometimes reaching a length of 6 feet.

In rivers of medium current, around 1 foot per second, with gravelly and partly silted beds, the flowering plants are much more numerous and various, and definitely zoned communities make their appearance, as in a pond. While there is a comparatively strong current in the centre of the stream it slows down as the banks are approached, and the quietness of the water near the shore allows the development of floating leaf and reedswamp communities. The submerged vegetation in the centre of the stream may include *Ranunculus fluitans* and *Sparganium simplex*, practically always pondweeds (*Potamogeton perfoliatus* and other species), and frequently, in well-silted streams, the submerged form of the arrowhead (*Sagittaria sagittifolia*, Phot. 107). In addition, there may be submerged shoots growing out into midstream from plants belonging to the floating leaf and reedswamp communities nearer the bank, for example yellow water lily (*Nuphar luteum*) and mare's-tail (*Hippuris vulgaris*).

The floating-leaf community (Phot. 108) commonly contains yellow water lily, the common pondweed *Potamogeton natans*, and *Polygonum amphibium*, a plant

R. W. Butcher

PHOT. 106. River Tees at Neasham (not silted). A water crowfoot (*Ranunculus fluitans*) dominant.

R. W. Butcher

PHOT. 107. River Lark, Suffolk (silted). Floating leaves of arrowhead (*Sagittaria sagittifolia*) and bur-reed (*Sparganium simplex*).

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A. H. Church

PHOT. 108. Floating leaves and reedswamp in the Thames above Oxford. Fringed water lily (*Nymphoides*) in front, yellow water lily in centre: river dropwort (*Oenanthe fluviatilis*) right, bur-reed (*Sparganium erectum*) behind.

which grows both in water, with its leaves floating, and also on land. Within the bounds of this community there are often plants whose inflorescences and parts of their vegetative shoots rise above the surface of the water. Among these are mare's-tail, arrowhead with its characteristic aerial leaves (Phot. 100), water plantain (*Alisma plantago-aquatica*), and in southern England a characteristic water dropwort (*Œnanthe fluviatilis*, Phot 108).

The reedswamp community is often dominated by bulrush (*Scirpus lacustris*), or by other species such as great bur-reed (*Sparganium erectum*, Phot. 108), common reed (*Phragmites vulgaris*), or the tall grass *Glyceria maxima*: close to the bank many other plants of similar habit are associated.

In rivers of medium to slow current (less than 1 foot per second) with sandy and silted beds, all the plants and communities already mentioned are found except those characteristic of very swift streams, and the vegetation is often so luxuriant as to block the stream in late summer unless it is periodically cleared. Canadian waterweed (*Elodea canadensis*), which once choked many of these streams, is still abundant—sometimes dominant in the submerged community—and the water starwort (*Callitriche stagnalis*) is generally frequent or abundant. Reedswamp of *Glyceria maxima* is characteristic of many of these rivers in the east and south of England, often accompanied by other tall grasses such as *Phalaris arundinacea*.

Where the current is very slow or negligible the vegetation approximates to that of a pond, as described on p. 208. Here the pondweed *Potamogeton lucens*, with oblong, very translucent leaves, is often dominant in the submerged community, and *P. pectinatus*, with filiform stems and very long filiform leaves, is also abundant.

In a very turbid river where the bed is unstable and the water full of suspended particles the light penetrating the water is so much diminished that submerged vegetation may be quite absent, though reedswamp of great bur-reed, bulrush, reedmace, arrowhead, etc., is often present.

CHAPTER XIV

MARSH AND FEN

In common language the words *bog*, *swamp*, and *marsh* are often used more or less interchangeably for any area of permanently wet ground covered with vegetation. On the whole, however, "swamp" is used when the summer water level is normally above the surface of the soil, while "bog" is applied particularly to the type of wet acid peat soil characteristically inhabited by "bog moss" (*Sphagnum*) and so common in Ireland (Chapter XI). The word "marsh" is here restricted to wet areas of mainly mineral soil, such as may often be found on the edges of lakes and large ponds and on the undrained flood plains of rivers. A fourth word, *fen*, is used for wet peat (i.e. purely organic) soil which is typically alkaline in reaction, though occasionally neutral or slightly acid. The East Anglian Fenland in north Cambridgeshire and adjacent counties is the largest area of English fenland, though only small fragments still bear natural vegetation, practically the whole of it having long been drained and cultivated; but smaller areas of fen are found in different parts of the country, some of them still in a natural state. Their alkalinity is due to the ground water being derived by drainage from calcareous rocks—in East Anglia the Chalk. The vegetation of marsh and fen is closely similar, though some of the fen species are calcicolous, i.e. mainly inhabiting calcareous soils; the dominant factor in both is the waterlogged but not markedly acid soil, often rich in mineral nutrients.

Where the ground outside the reedswamp on the edge of a pond, lake, or river is flat and waterlogged, marsh plants naturally succeed reedswamp plants, the free growth of whose rhizomes in the soft mud on the edge of the water being hampered by the more compact soil of the marsh, which is often more or less grazed and trampled. As the marsh plants begin to colonise the ground, the reedswamp plants die out. Exceptions do, however, occur. Thus the

common reed (*Phragmites*), a very widespread dominant of reedswamp, can maintain itself in marshland, and species of rush (*Juncus*), which occasionally form reedswamp, are more characteristically marsh or wet grassland plants. Many subordinate species, also, may be found both in reedswamp and marsh.

The flood plain of a river under natural conditions is, of course, subjected to the intermittent deposit of silt by the overflowing waters of the stream, generally in winter, so that the soil level is gradually raised above the summer water level. Succession to drier soil communities takes different courses according to the incidence of other factors. The surface of the flooded area tends to dry out during the summer, and grasses and herbs not confined to wet soil begin to settle down among the marsh plants. This type of ground forms the characteristic alluvial meadowland which is cut for hay or grazed, and whose fertility is maintained by the silt from the winter floods. The access of the silt-bearing floods to these "water meadows" used often to be regulated by a system of sluices and ditches. The natural succession is thus stopped at a grassland stage by the intervention of the human factor.

In the absence of such intervention the marsh is naturally colonised by woody plants—shrubs like the different kinds of sallow, and trees such as the crack and white willows (*Salix fragilis* and *alba*),[1] birch, and alder; and because of its stature and of the shade which it casts alderwood is the natural climax of these marsh woodlands. Alderwoods must at one time have been very extensive on the wet flood plains of rivers, but owing to drainage, grazing, and cultivation these have almost entirely disappeared from the rich alluvial lands, which have naturally been exploited wholesale for the uses of agriculture—either as meadowland or arable. Here and there, however, on patches of wet land, fragments of natural alderwood remain, and these contain a characteristic accompanying flora of marsh plants which can bear shade, conspicuous among which is the

[1] These are often planted along the banks of rivers to consolidate the soil and prevent its being washed away in times of flood. Pollarded willows fringing slow rivers and dykes are a familiar feature of low-lying alluvial land.

great stooled sedge *Carex paniculata*. A belt of alders is also commonly seen fringing the small streams that meander through the agricultural lowlands. Alders were not uncommonly planted and coppiced in such situations, largely because of the use of their wood in the manufacture of the old black gunpowder, and in the north of England for clogs; and alder coppices of this origin are still occasionally seen. Osiers (*Salix viminalis*, the common osier, with very long narrow leaves, and *S. purpurea*, the purple osier, with broader, glaucous leaves) are often planted in the same situations. Alder is often accompanied by ash and birch in these marsh woods, which have been described in Chapter VIII, and the pedunculate oak sometimes establishes itself, suggesting a transition to damp oakwood. Species of poplar (*Populus canescens*, grey poplar, and *P. nigra*, black poplar) are occasionally found in these woods in southern and eastern England.

The raising of the soil level by repeated silting is, of course, limited to the area on each side of a river reached by periodic flooding. On the other hand, rise in the surface resulting from the accumulation of humus is not so limited, and in any case humus always accumulates in our climate where plant-growth is continuous and the vegetation is not removed by felling, cropping, grazing or burning. In this way, no doubt, by the accumulation of better aerated humus, mixed with and on the top of the silt, the marsh woods may actually have been succeeded by damp oakwoods as the surface humus rose above the ground water level.

In flat lakeside and riverside areas where silting is at a minimum or practically absent the rise of the soil surface is due almost entirely to the accumulation of humus. Since the humus is waterlogged for most of the year, and is therefore badly aerated, decay of the plant remains is arrested and peat formation results. In the most characteristic of such areas the ground water comes from calcareous rocks and is therefore rich in lime, so that the peat is distinctly alkaline in reaction. This is typical *fen peat*, and the vegetation it bears differs entirely from bog peat (pp. 88, 184-5), and is closely akin to marsh vegetation. While the marsh succession is nearly always radically interfered with by man, there still remain examples of fen

succession which are substantially natural, so that we can trace the successive stages.

Nevertheless, much of the apparently "natural" extent of herbaceous fen vegetation, such as occurs, for instance, round the Broads of East Norfolk, or at Wicken Fen in Cambridgeshire, owes its present state to human activity. A herbaceous fen community is in fact a natural stage in the succession from water to land vegetation, but under natural conditions it is limited to the belt between summer and winter water levels. Below the summer water level, i.e. where normally there is free water standing above the soil throughout the year, we have reedswamp: above the winter water level, i.e. where the peat surface is normally free from standing water throughout the year, woody plants colonise the peat and rapidly establish fen scrub—*carr*, as it is called—and eventually, if seed parents are present, fen woodland. Between these is a belt of herbaceous fen vegetation. If, however, the seedlings of shrubs and trees above the winter water level are constantly destroyed by mowing, carr cannot develop and such mown areas remain as herbaceous fen. The inhabitants of fen districts habitually cut the reeds which dominate many tracts of fen for thatching, and the sedge and grass vegetation for litter, and in this way wide areas of fen above the winter water level were maintained as herbaceous fen over and above the belt between the summer and winter levels which would always be dominated by the herbaceous fen plants. At places like Wicken Fen this belt is comparatively narrow because the extent of winter flooding is rather strictly controlled by a system of pumps and sluices, so that the average winter rise of the water is only about 12 inches (30 cm.) and almost the whole extent of the fen is above the normal winter water level. But in some other regions, such as the fenland around Lough Neagh in Northern Ireland, the winter flooding is much deeper, from 1 to 2 metres, and the extent of "natural" fen correspondingly greater.

The reedswamp communities of the northern Norfolk Broads are dominated by common reed (*Phragmites*), narrow-leaved reedmace (*Typha angustifolia*), and in places the bulrush (*Scirpus lacustris*) on the side towards the open

water. In the Yare valley these are replaced by the tall grasses *Glyceria maxima* and *Phalaris arundinacea*, corresponding, probably, with heavier silting and a richer supply of nutrient salts. Of these plants, the common reed and *Glyceria* extend into and often dominate the adjoining fens, i.e. they maintain themselves after the peat has reached the summer water level. A widespread plant, especially in East Anglia, forming nearly pure communities in the transition from reedswamp to fen, is the saw sedge (*Cladium mariscus*), which colonises the very shallow water of closed reedswamp and rapidly builds up the peat to the surface of the water, where it maintains itself just above the summer water level. *Cladium* has strap-shaped evergreen leaves which may be as much as 9 feet long and have sharp cutting serrated edges. These immensely long leaves bend over about the middle and live for two or three years. When they die they decay very slowly, remaining propped among the living leaves and forming a continuous thick elastic "mattress." Owing to this habit, saw sedge excludes most other plants, and in the Cladietum at Wicken there are only a few scattered individuals of the tall yellow loosestrife (*Lysimachia vulgaris*), dwarf creeping willow (*Salix repens* var. *fusca*), and common reed (*Phragmites*), the last maintaining itself for a long time in the fen by means of its vigorous and extensive underground rhizomes which push horizontally below the surface of the peat and send up vertical shoots at intervals.

These very pure dense communities of saw sedge were regularly cut by the fenmen for thatching and kindling. If the cutting is done not oftener than once in four years the community can maintain itself apparently indefinitely, but if it is cut more often, say once in two years, the plant is enfeebled by the frequent removal of the living leaves, and the purple moor-grass (*Molinia caerulea*) enters the community and comes to share dominance with *Cladium*. This community is known as "mixed sedge." Other plants, besides loosestrife and reeds, come in at the same time, for example the tall angelica (*Angelica silvestris*), a common plant of damp oak woodland, hemp agrimony (*Eupatorium cannabinum*), milk parsley (*Peucedanum palustre*), which is the food plant of the swallow-tail butterfly, and the

little creeping marsh pennywort (*Hydrocotyle vulgaris*) with its circular leaves. These accompanying plants are conspicuous after the cutting of the sedge, but tend to be crowded out as *Cladium* and *Molinia* resume dominance. If the sedge is cut every year the *Cladium* succumbs and *Molinia* remains dominant alone. This community (Molinietum) used to be cut for cattle bedding by the fenmen, who call it "litter." The *Molinia* is not injured by the frequent cutting, because only the dead leaves remain when it is cut in autumn. In the Molinietum accompanying plants are more abundant and include meadow-sweet (*Filipendula ulmaria*), meadow-rue (*Thalictrum flavum*)—a tall plant with finely cut leaves and loose inflorescences of numerous small pale yellow flowers—devil's bit (*Succisa pratensis*), the smaller valerian (*Valeriana dioica*), and the rather uncommon spineless thistle, *Cirsium anglicum*, with handsome solitary heads of crimson florets.

Thus while the pure Cladietum is a natural and regular stage in the fen succession, Cladio-Molinietum and Molinietum are semi-natural communities brought into existence by repeated cutting and consequent enfeeblement of the Cladietum.

In any wide extent of herbaceous fen there is a great variety of species corresponding with the variety of habitat provided by the unevenness of the fen surface and the different modes of growth of different species, some forming large tussocks rising well above the water level, in the interstices of which a drier humus is formed, while the wet peat between the tussocks is colonised by the more hydrophilous (water-loving) fen plants. Another cause of variety is the different treatment of different areas by the fenmen, some being repeatedly cut, others more seldom, as in the case of the *Cladium* and *Molinia* communities at Wicken which have just been described. Besides these two the common reed (*Phragmites*), and in areas richer in silt, like the Yare valley, *Glyceria* and *Phalaris*, establish dominance over wide stretches of fen. Two other very abundant fen plants, sometimes rising to local dominance, are a characteristic fen rush, *Juncus subnodulosus*, and a sedge, *Carex panicea*. Of plants with conspicuous flowers—some common in almost any wet soil, others confined or

almost confined to fen—we have marsh marigold (*Caltha palustris*), marsh cinquefoil (*Comarum palustre*) with large purplish flowers, the beautiful marsh helleborine (*Epipactis palustris*), the marsh orchis (*Orchis incarnata*), marsh pea (*Lathyrus palustris*), yellow flag (*Iris pseudacorus*), ragged robin (*Lychnis flos-cuculi*), the tall purple loosestrife (*Lythrum salicaria*), and the yellow loosestrife (*Lysimachia vulgaris*). The rare fen orchid *Liparis loeselii* is another notable species. The fen fern *Dryopteris thelypteris* is abundant. Photograph 109 shows six of these characteristic fen species. Photographs 110 to 112 show examples of "mixed fen" (and reedswamp) probably due to repeated cutting, with a variety of flowering plants.

Woody plants colonise the herbaceous fen with great rapidity. Two low-growing woody species—sweet gale or bog myrtle (*Myrica gale*), which occurs also in some bogs, and a creeping willow (*Salix repens* var. *fusca*)—belong with the field (herbaceous) stratum of the fen vegetation because of their low stature, but bushes of other species come in close above the winter water level in any area which is not repeatedly cut. In a small patch closely studied at Wicken alder buckthorn (*Frangula alnus*) was the earliest mass invader and it dominates the young "carr," as the fen scrub is called. It is commonly accompanied by the grey sallow (*Salix atrocinerea*). Somewhat later come guelder rose (*Viburnum opulus*), and common buckthorn (*Rhamnus catharticus*), which dominate the older carr. The sallow appears to be comparatively short-lived, and alder buckthorn suffers severely from "die-back" caused by the attacks of two fungi; and this is an important factor in its loss of dominance in the older carr. Privet (*Ligustrum vulgare*) is locally abundant, and hawthorn (*Crataegus monogyna*) is frequent. Trees are rare in the carr at Wicken Fen, no doubt because it is part of a patch of fen vegetation long isolated in the midst of arable land in which there are few trees to act as seed parents. In the fens of East Norfolk alder and birch are abundant in the developing carr (Phot. 114), ash is frequent, and oak occasional.

The saw sedge maintains itself at first between the bushes of the developing carr, but as the canopy closes it is gradually suppressed. The dead leaves may be found for

M. Pallis

PHOT. 109. Fen in East Norfolk. In front are seen fen fern (*Dryopteris thelypteris*), fen rush (*Juncus subnodulosus*), marsh helleborine (*Epipactis palustris*) in flower; and yellow loosestrife (*Lysimachia vulgaris*) and yellow flag (*Iris pseudacorus*) not in flower. Behind are the densely packed shoots of the common reed (*Phragmites communis*).

J. Massart

PHOT. 110. Floating clump of *Glyceria maxima*, with reedswamp and carr behind, on the edge of Rockland Broad, Norfolk.

J. Massart

PHOT. 111. Reedswamp of narrow leaved reedmace (*Typha angustifolia*), with water parsnip (*Sium*), cowbane (*Cicuta virosa*), etc.

C. G. P. Laidlaw

PHOT. 112. "Mixed fen" in East Norfolk. This is usually the result of very frequent cutting and contains many species not common in typical fen. Here the two water parsnips (*Sium erectum* and *S. latifolium*) are conspicuous, with various sedges (*Carex*).

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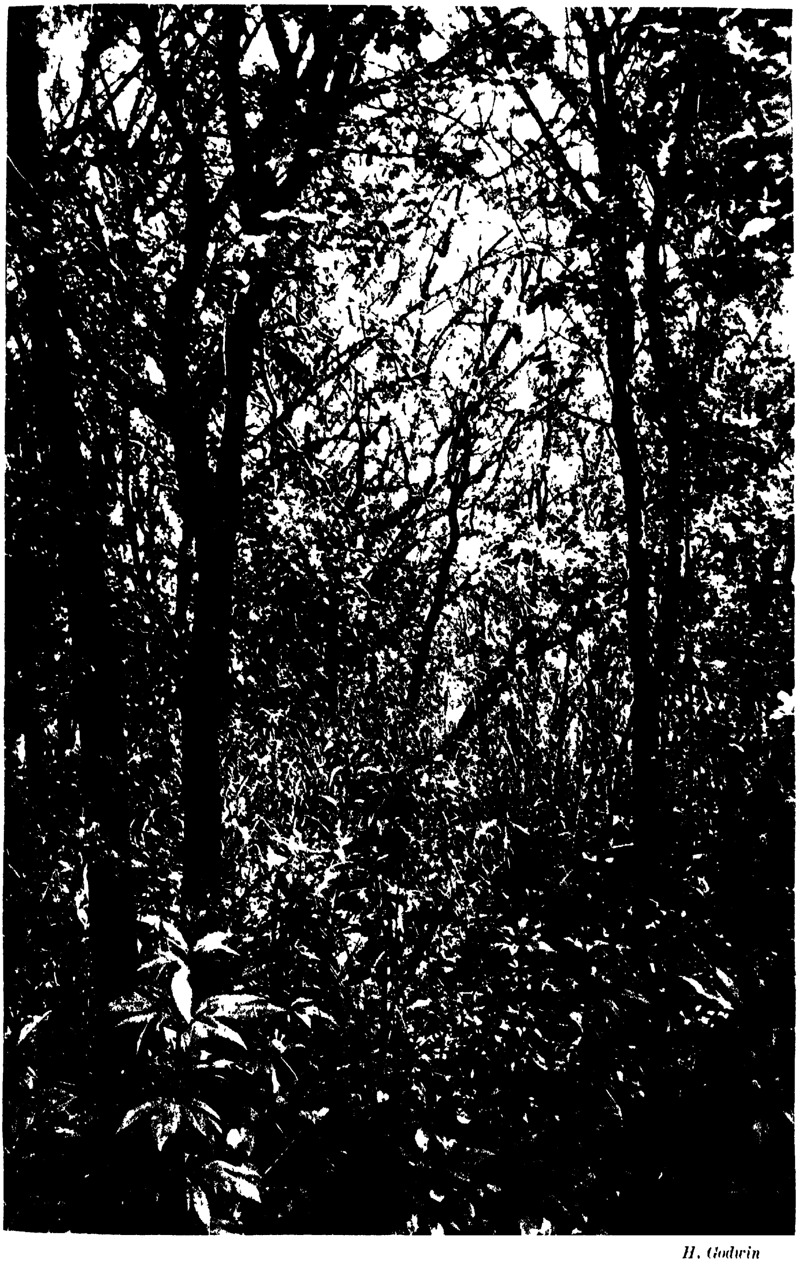

H. Godwin

PHOT. 113. Mature buckthorn carr (*Rhamnus catharticus*) at Wicken Fen, Cambs. Hemp agrimony (*Eupatorium cannabinum*), yellow flag (*Iris pseudacorus*), dewberry (*Rubus caesius*) and stinging nettle (*Urtica dioica*), are seen in the field layer.

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M. Pallis

PHOT. 114. Carr developing on fen in East Norfolk. Ash (*Fraxinus excelsior*), birch (*Betula pubescens*), sallow (*Salix atrocinerea*). Common reed dominates the fen, with fen rush and sweet gale (*Myrica gale*).

G. E. Briggs

PHOT. 115. Young carr of alder buckthorn (*Frangula alnus*) at Wicken Fen. The persistent leaves of the saw-sedge (*Cladium*) from the preceding Cladietum are caught in the crotches.

a long time in the carr, sometimes caught up in the crotches of the shrubs (Phot. 115). In time the ground becomes quite bare and is then recolonised by a very characteristic set of species, none of which, however, flowers in the dense shade. The most abundant of these at Wicken are the fen fern (*Dryopteris thelypteris*), dewberry (*Rubus caesius*), and creeping bent-grass (*Agrostis stolonifera*). Bindweed (*Calystegia sepium*), yellow flag (*Iris pseudacorus*), and yellow loosestrife (*Lysimachia vulgaris*) are also abundant, with comfrey (*Symphytum officinale*), hemp agrimony (*Eupatorium cannabinum*), and common stinging nettle (*Urtica dioica*) frequent. The mosses *Hypnum cuspidatum* and *Mnium affine* are common in the ground layer. Photograph 113 is a view inside the buckthorn carr at Wicken. The carrs of the East Norfolk fens, which are dominated by alder or birch, and which may eventually pass into wet oakwood, have been described in Chapter VIII, pp. 120-122.

Thus in the climate of East Anglia the fen succession finally leads, or would lead if it were not for human intervention, to the establishment of forest; but here and there on the fens a different trend of development is seen. This is the local formation of acid humus, above the level of influence of the alkaline ground water, for example in the interstices of tussock-forming plants like *Cladium* or *Molinia* or of the stool-forming species of *Carex*. Here species of bog moss such as *Sphagnum cymbifolium* and *S. squarrosum* may settle down and form acid peat in which plants like the sundews (*Drosera rotundifolia* and *D. anglica*), narrow-leaved cotton-grass (*Eriophorum angustifolium*), and the hair-moss *Polytrichum commune* find a footing. These plants are not those which grow only in the most acid soils, but are intermediate in mineral requirements between the fen plants and typical bog plants. This kind of local development occurs in many places in the fens of East Norfolk, and represents a stage in the formation of raised bog as described in Chapter XI, pp. 184-8. There is good evidence that in the past raised bog was actually formed on the East Anglian fens, at least towards their edges.

In the much wetter climate of north-western England, as in the Lake District, the small local "fens" do not show a general tendency to the development of forest. To begin

with, their ground water is rarely alkaline, since it does not drain from calcareous rocks but from siliceous rocks poor in bases. But since the vegetation and its early development may be very similar to that of typical fen, it is included in the same general category. The similarity is especially marked when the fen is heavily silted, as on the banks of a stream or beck where it flows into a lake. The beck brings down abundant inorganic silt, and when it is in flood the silt is deposited on adjacent flat ground as well as in the lake round the mouth of the beck. Reedswamp of reed, bulrush, and reedmace is developed on the edge of the water, and this is succeeded by fen dominated by reeds, by various species of sedge, and where the silt is most abundant and acidity least, by the tall grasses *Phalaris arundinacea* and *Calamagrostis*, accompanied by many other fen plants such as yellow flag, meadow-sweet, and the two loosestrifes. Here the good supply of nutritive mineral salts in the silts has an effect on the vegetation similar to that of the alkaline waters of typical fen, though the water is distinctly acid.

Where silting is less and acidity greater, the common reed (*Phragmites*) is followed by *Molinia*. Carr may be formed, composed mainly of the grey sallow and other willows, but this appears to be transitory and is not followed by forest development. In these less silted areas sweet gale (*Myrica*) accompanies *Molinia*, and eventually bog plants colonise the Molinietum, *Molinia* gradually disappearing and raised bog developing.

Round the shores of Lough Neagh in north-eastern Ireland there are extensive areas of fen. The waters of this lake are about neutral, and those of drains cut through the fen peat slightly, but never extremely, acid. This is because the rivers flowing into Lough Neagh come partly from basalts, and the lime which they carry forms what is called an alkaline "buffer," preventing the development of any marked acidity in the fen water, though the climate certainly favours the development of acid bog and moor vegetation. The flora of the Lough Neagh fens is very much like that of the East Anglian, though some species are absent, and others, for example the saw sedge and the common buckthorn, are rare or local. It does not seem

that the mowing of the vegetation is anything like so extensive and systematic as in East Anglia, and the great extent of the fen is due to the deep winter floods which cover wide areas. A feature of these fens is the great fragmentation, so to speak, of the vegetation, a large number of more or less distinct societies being recognisable at different levels. This is probably because the very extensive peat cutting, carried to different depths in different places, has established a series of distinct graded habitats in relation to the water level, each especially suited to the dominance of particular fen species.

The highest of these fen societies towards the upper level of the winter floods are dominated by meadow-sweet, species of rush (*Juncus*), and purple moor-grass or "flying bent" (*Molinia*), and their peat is more acid. Here, as the alkaline buffering of the fen water diminishes, species of bog moss (*Sphagnum*) and other acid-loving plants establish themselves.

Woody vegetation may colonise the fen, and such scrub as occurs is dominated by sallows. Though other shrubs and trees, including birch and alder, are found in the fen, it is evident that the development of dense carr and alderwood does not occur, as it does in East Anglia. In other words, the natural successor of fen in north Ireland, as in the English Lake District, is not forest, but bog and moor.

CHAPTER XV

MARITIME VEGETATION

Salt Marsh

THE vegetation of our sea coasts contributes some of the most attractive elements to Britain's Green Mantle. The habitats are very varied, ranging from coastal rocks and lofty cliffs to the great stretches of salt marsh, the changing topography of sand-dune areas, and the more limited but highly interesting shingle beaches. The sea cliffs are the most striking scenically, but the beauty of marshes and dunes always remains in the memory of those who have frequented them and have watched the ebb and flow of the sea over the wide expanses of marsh at a high spring tide in the changing lights of a spring or autumn morning or evening, or the scurries of sand on the mobile dunes in a gale which tears it out from one place and piles it up in another.

Coastal vegetation is essentially dynamic, continuously changing because of the continual changes of its habitats. Cliffs are gradually eroded by the sea—very slowly where they are made of hard rock, quite rapidly where they are of clay, sand, or chalk. Salt marshes and sand dunes, on the other hand, are essentially areas of accretion, the land gaining on the sea by the accumulation of mud and sand brought in by the tide and by the piling up of blown sand on the dunes. In these changes the plants which inhabit the marshes and dunes play an indispensable part, mainly by stabilising the newly added soil, and different kinds of plants live and are active in successive zones of marsh and dune. Thus the coastal plant communities provide an unrivalled opportunity for the study of the succession of vegetation.

The three main types of "accretional" habitat—tidal marsh, dune, and shingle beach—are commonly found in close association, and are linked together through the processes which build them up. Shingle spits and dunes often protect salt marshes, dunes are often built on shingle.

The whole complex of habitats forms one of the most fascinating and instructive subjects of study in the field of plant ecology.

Vegetation which is more or less profoundly affected by the neighbourhood of the sea is here called *maritime*, in contrast with that which actually lives in the sea (*marine*). This cannot be an absolute distinction, because plants which are covered by the sea at the highest tides but are exposed to the air at low tide are clearly intermediate between them. The belts of vegetation inhabiting the intertidal zone of rocky coasts are, however, fairly reckoned as marine because most of them are algae ("seaweeds"), not only covered with sea water for a large part of the time, but with their active vegetative life adapted to the conditions of submergence, while the vegetation of sand or mud flats, only covered by the higher tides and dominated mainly by flowering plants whose active life is subaerial, may properly be called maritime. Besides this "salt-marsh" vegetation, the plant communities of coastal sand dunes and shingle beaches, which are not normally reached by any tides, must also be included as maritime, because they are considerably affected by the neighbourhood of the sea though not immersed in sea water; and so must the vegetation of rocks and sea cliffs which are above the reach of the highest tides but are constantly subject to sea spray when there is a strong onshore wind. Finally, the vegetation of grassland on cliff-tops, less strongly affected by spray, and the plants of brackish waters and marshes behind the actual coast, may be called *submaritime*.

Plants adapted to the effects of salt water in the soil or of salt-laden spray are called *halophytes*,[1] and a common structural characteristic is succulence of the plant body, owing to the presence of abundant "water tissue" whose cells are large, thin-walled, and swollen with cell sap which contains great quantities of salt. Salt-marsh plants are typical halophytes, while sand-dune plants are not.

THE SALT-MARSH COMMUNITIES

Salt-marsh vegetation occupies the mud and sand of those marginal parts of tidal estuaries or bays which are pro-

[1] "Salt plants," from the Greek ἅλς, salt.

tected from swift tide races and currents. On exposed coasts, and wherever the sand and mud is violently moved by waves or currents, rooted plants cannot, of course, establish themselves.

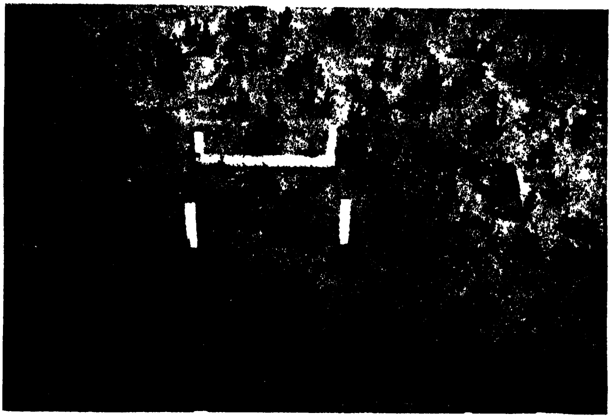
The salt-marsh formation is very definitely *zoned*, i.e. it is composed of successive communities as we pass from the lowest ebb-tide levels towards the land. The surface soil of the upper parts of the "marsh" is dry for much the greater part of the time, so that it is easy to traverse. It is not generally realised that even the lowest salt-marsh communities, where the sand or mud is decidedly wet, are covered by the sea for much less than half the time, while the uppermost ones, reached only by the highest spring tides, are covered for a total period of only about three hours in the month during spring and autumn, and not at all throughout the summer.

The first colonists of the mobile sand or mud below the level reached by high water of the neap tides,[1] so that they are covered for some time every day throughout the year, are certain kinds of green algae (*Rhizoclonium*, *Enteromorpha*, etc.). This zone is sometimes dominated by "sea grass" or sea wrack (*Zostera*), a marine monocotyledon[2] with very flexible band-shaped leaves, excellent when dried for stuffing mattresses. The whole of these great fields of sea grass are exposed when the spring tides recede far below the level of the lowest salt-marsh community.

The first community belonging to the salt marsh proper consists almost entirely of the glasswort or marsh samphire (*Salicornia herbacea*), a highly succulent erect annual plant whose cylindrical shoots are composed of well-marked segments, each segment consisting of two opposite succulent leaf bases without blades, quite concealing the central stem. The glasswort seeds germinate readily in the soft mud which has been partially stabilised by the pioneer algae, but they can scarcely maintain themselves where they are disturbed daily by the incoming tide, which drags them from their anchorage. Two or three days undisturbed by

[1] Neap tides are the tides of least range, which neither rise so high nor fall so low as the spring tides.

[2] The monocotyledons are the class of flowering plants to which palms, lilies, orchids, grasses, sedges, etc., belong. They often have long band-shaped leaves with parallel veins.

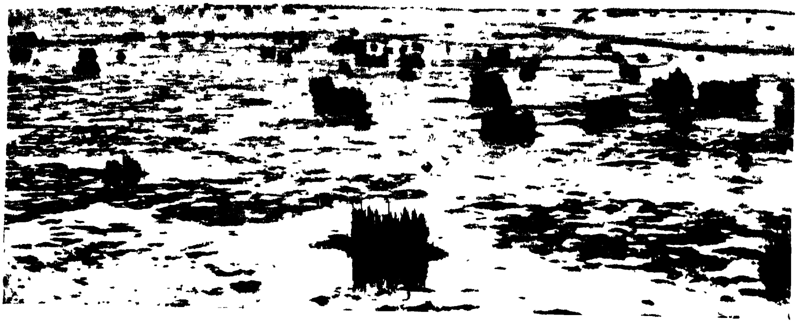


P. O. White

PHOT. 116. Sparse Salicornietum just above the range of daily tides, Dovey salt marshes.

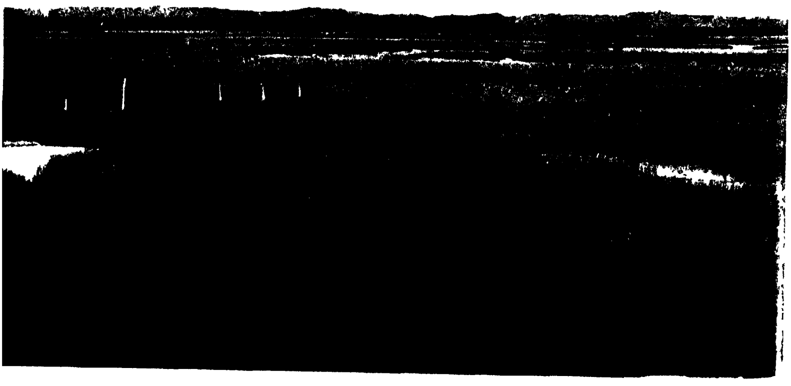
R. H. Yapp

PHOT. 117. Salicornietum with primary depression pan, Dovey salt marshes.



R. V. Shearing

PHOT. 118. Hole's Bay, Poole Harbour, June 1911. Rice-grass (*Spartina townsendii*) colonising the soft mud.



F. W. Oliver

PHOT. 119. The same view, June 1924. Dense Spartinetum has completely covered and con solidated the mud.

the tide are necessary for the establishment of at all a continuous Salicornietum.

Glasswort often grows in a practically pure community (Phots. 116, 117), but it is frequently accompanied by the sea manna-grass (*Glyceria maritima*), the most abundant and characteristic of the salt-marsh grasses and commonly occurring through a considerable range of the marsh. Other plants that may be found in the Salicornietum are the sea blite (*Suaeda maritima*), particularly on sandy soils, and the sea aster (*Aster tripolium*), whose handsome heads of flowers with yellow centres and lilac rays are conspicuous ornaments of the marsh on soft open mud at various levels. Both sea blite and sea aster are markedly succulent plants.

At various points on the coast, but especially in Southampton Water and Poole Harbour, where the tidal silt is a thick viscous mud, the tall strongly growing rice-grass (*Spartina townsendii*) replaces *Salicornia*, and it can colonise deep mobile mud, often too mobile for the successful establishment of Salicornietum. The rice-grass is a hybrid between the American species *Spartina alterniflora* and the European *S. stricta*. It was first recorded from Southampton Water in 1870, and since then has increased its area very rapidly, covering great stretches of mud with pure dense vegetation, since no other species can compete with it in its special habitat. Thus it can be used for "reclaiming" tidal mud. The extraordinary transformation it can bring about in a few years can be well seen by comparing Photograph 119 with Photograph 118. The leaves offer broad surfaces to the silt-bearing tidal water, and their points catch and hold fragments of seaweed and other flotsam. The thick forest of stems and leaves breaks up the tidal eddies, preventing the removal of mud that has once settled on the marsh. The level of the soil is thus continually raised, the tidal currents and channels profoundly altered, and the whole aspect of the intertidal zone completely changed. No other species of salt-marsh plant, at least in north-western Europe, has anything like so rapid and complete an effect in gaining land from the sea.

The upper edge of the Salicornietum (where *Spartina* is absent) is invaded and the glasswort eventually replaced

as a dominant either by the sea manna-grass or the sea aster. *Glyceria maritima* is a vigorous perennial grass which "tillers" (i.e. forms lateral propagating shoots) very freely, and under grazing quickly forms a turf. This Glycerietum is the basis of many of the famous salt-marsh sheep pastures (*près salés*). Excellent examples are seen on the flats at the mouth of the Dovey estuary in Cardiganshire. At first it often makes low hummocks by catching and accumulating sandy mud, thus restricting the space available for *Salicornia.* The hummocks eventually coalesce and raise the general level of the soil. Photograph 120 shows an ungrazed example. Besides the glasswort and sea aster, other species of salt-marsh plants, more abundant at higher levels, often occur in the Glycerietum, for example scurvy-grass (*Cochlearia officinalis*) and sea plantain (*Plantago maritima*). In some marshes in which *Glyceria* is absent or plays but an insignificant part the Salicornietum is invaded in quantity by the sea aster, which may become dominant.

All these communities belong to what may be called the " lower salt marsh," subject to submergence by the tide for more than 50 hours in the month, and almost all the plants belonging to them are decidedly succulent. We now come to the communities of the "middle marsh," which often occupy great areas of almost flat ground, the soil of which remains uncovered by the tide for long periods during the summer. Here two species with very attractive flowers often play a conspicuous part. One of these is the common sea lavender (*Limonium vulgare*), whose lavender-purple blossoms make glorious sheets of colour in middle and late summer, for instance on parts of the coast of Morecambe Bay. Sea lavender commonly invades the Glycerietum and becomes co-dominant with the sea manna-grass. Species of the lower zones, such as glasswort, sea aster, and sea blite, usually persist in smaller numbers in the Limonietum, and others appear, such as the sea plantain (*Plantago maritima*), which is a common plant of the middle and upper marsh, ranging right up to the Juncetum (see below), and the sea spurreys (*Spergularia marginata* and *S. salina*) with their small starlike white or pinkish flowers.

The other conspicuous dominant of the middle marsh

H. S. Thompson

PHOT. 120. Glycerietum, unpastured, with flowering clump of sea aster (*Aster tripolium*) in the centre, and of sea arrow-grass (*Triglochin maritimum*) to the left. Berrow mud flats, Somerset.

R. H. Yapp

PHOT. 121. Pastured Glycerietum with hummocks of thrift (*Armeria*). Primary pan in the foreground. Dovey salt marshes.

R. H. Compton

PHOT. 122. Mixed salt marsh at Holme-next-the-Sea, Norfolk. Sea purslane (*Obione portulacoides*), left; matted sea lavender (*Limonium reticulatum*) in flower, right; sea spurrey (*Spergularia marginata*), three flowers, centre; also *Glyceria maritima*, sea plantain, common sea lavender and thrift.

R. H. Yapp

PHOT. 123. Obionetum succeeding Glycerietum near Gedney Drove End, the Wash.

often comes in at a slightly higher level than sea lavender. This is thrift or sea pink (*Armeria maritima*) with its heads of rose-pink flowers, which begin to appear in April and are at their best in May and June, giving a show of colour comparable in beauty with the purple sea lavender later in the summer. Thrift is a strongly tufted and deeply rooting plant which at first forms isolated silt-trapping hummocks in the Glycerietum (Phot. 121). It stands grazing well, and with *Glyceria* often forms the foundation of the sheep pastures of the middle marsh. It does not tolerate so much salt in the soil as the dominants of the lower marsh and grows more vigorously with decreasing salt content, so that it is frequently found in the turf of sea cliffs or other maritime grassland. The subordinate plants of the Armerietum are much the same as those of the Limonietum.

Though sea lavender and thrift are often separately dominant at two slightly different levels, there is frequently a considerable mixture of species in the middle marsh, rather than any pronounced dominance of one or two, and the vegetation so composed has been called the "general" or "mixed" salt-marsh community (Phot. 122). The following six species are most frequently represented: sea lavender, thrift, sea manna-grass, sea spurrey, sea arrow-grass (*Triglochin maritimum*), shrubby sea purslane (*Obione portulacoides*).

The last-named plant, a mealy, greyish-white undershrub, plays an important part in many salt marshes, especially on the east coast, where it becomes overwhelmingly dominant in certain habitats (Phot. 123). It flourishes in a well-drained soil, where it roots deeply, and particularly affects the banks of deeply cut drainage channels. From this position it may spread over the drier middle and upper marshes, covering the ground with a thick greyish carpet 1 or 2 feet deep and almost completely obliterating the other vegetation.

Another woody plant, the shrubby sea blite (*Suaeda fruticosa*), is a Mediterranean plant which is found only in a few places, but very abundantly where it does occur, on the south and east coasts of England. This is a bush 2 or 3 feet high with narrow dark green leaves and, like *Obione*, seems to depend on good drainage. It is specially characteristic

of the edges of shingle beaches where they abut on salt marsh (Phot. 141 and p. 253). Associated with *Suaeda fruticosa* at certain places on the east coast, as at Blakeney Point in north Norfolk, are two other Mediterranean species, the "sea heath" (*Frankenia laevis*) with narrow rolled leaves and 4-petalled rose-coloured flowers (Phot. 124), and *Limonium reticulatum*, a sea lavender with much branched inflorescences bearing small, crowded, pale lavender flowers (Phot. 122).

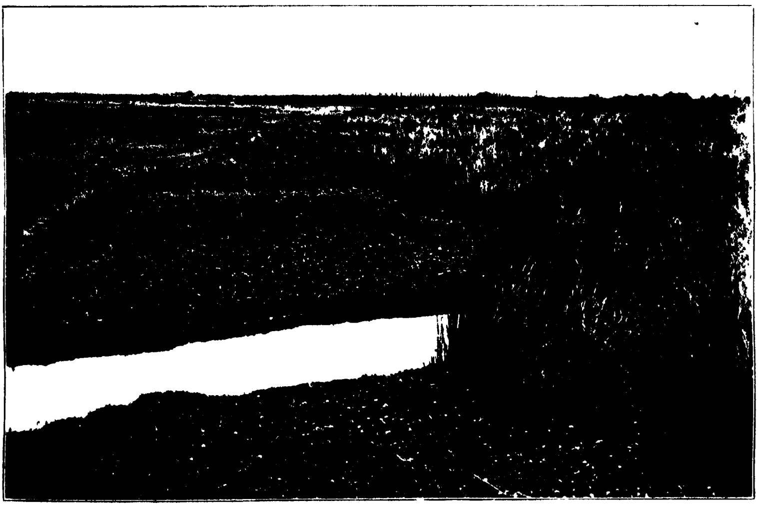
Where the soil is very sandy, *Glyceria maritima* often gives way in the upper marsh to a maritime form of the red fescue (*Festuca rubra*) which makes equally good sheep pasture. The accompanying species include some of the middle marsh, such as thrift, spurrey, and arrowgrass, together with others characteristic of the upper marsh, such as the stag's-horn plantain (*Plantago coronopus*) with acutely lobed leaves, the rather succulent sea milkwort (*Glaux maritima*) belonging to the primrose family, and a maritime rush (*Juncus gerardi*).

On the upper edge of many undisturbed salt marshes there is developed a zone of the sea rush (*Juncus maritimus*, Phot. 125). This grows much taller than any of the accompanying species and tends to destroy the close turf of the pastured Armerietum or Festucetum, providing more open soil and maintaining damper air between the tufts of rushes. As a result, many plants of the lower and middle marsh tend to reappear in the Juncetum, such as species of glasswort, sea aster, scurvy grass, and sea plantain: also various green, blue-green, red, and brown algae.

The surface of the later stages of the lower marsh, i.e. after the glasswort community has been invaded by *Glyceria* and other plants, is never quite uniform, because of the unequal growth and silt-trapping powers of different salt-marsh species. Thus there comes about a formation of low flat hummocks by the plants which hold most of the silt, and the ebb and flow of the tide tends to take a winding course round the larger hummocks. The hummocks extend horizontally as well as vertically and often coalesce into low ridges or considerable flat areas, while their growth in height slows down. The channels taken by the tide

J. Massart

PHOT. 124. "Sea-heath" (*Frankenia laevis*) in mature salt marsh.



R. H. Yapp

PHOT. 125. Sea rush (*Juncus maritimus*) community (right) abutting on grazed sward of red fescue and thrift (in flower). Dovey salt marshes.

R. H. Yapp

PHOT. 126. Mature salt marsh used as sheep pasture showing drainage channels and pans. Dovey salt marshes.

R. H. Yapp

PHOT. 127. Compound pan formed by enlargement and fusion of simple ones in compact turf of thrift or sea-pink (*Armeria maritima*) in flower. Dovey salt marshes.

between the hummocks, which are at first shallow and shifting, are gradually deepened along certain lines by the flowing water, and thus permanent channels are formed which persist in the middle and upper marsh. A high spring tide rushes up the channels with considerable force, especially if it is backed by a strong wind, but most of the erosion occurs at the ebb. The growth of the plants on the edges of the older and deeper channels, especially of *Obione*, which grows most luxuriantly in this well-aerated habitat, increases their power of trapping silt, and thus the banks of the channel rise, while its bed is deepened by the scour of the water. In this way regular systems of drainage channels comparable with river systems are established in the older marshes. The greater the tidal range and the difference of altitude between the bottom and top of the marsh, the stronger the scour and the deeper the channels.

Owing to various causes, such as the shifting of tidal currents, the flow of water up and down a particular channel may become insufficient to keep its bed scoured and clear of vegetation. The channel is then invaded by marsh plants, and sometimes bridged across the top, for example by stolons of *Glyceria maritima.* Thus parts of such a dormant or semi-dormant channel may "grow up" or be "roofed over" by marsh vegetation. The roofing in of a channel which still conducts a certain amount of water results in its becoming subterranean for parts of its course. Completely dormant channels may be quite obliterated.

If the hummocks of a group formed in a primary marsh coalesce so as to surround an area which then forms a relative depression, the water is hindered from draining away at the ebb and a primary "pan" is formed in which water remains after the ebb. If the substratum is sufficiently permeable this water may slowly percolate away, but, if not, it may remain, slowly evaporating, from one spring-tide cycle to the next, the water level rising, of course, if there is heavy rainfall. Such "pans" are normally bare of vegetation, probably because of their stagnancy and the great variations of salt concentration due to alternate evaporation and precipitation (Phots. 117, 121).

These primary pans are often transitory, but some persist into later stages of marsh development, and these are

generally remarkably stable and permanent, e.g. in the *Armeria* sward (Phot. 126). Secondary pans are formed in the way described above by the blocking up of insufficiently drained channels through the extension of vegetation across them. Secondary pans formed from parts of channels are recognised by their seriation, marking the course of the former channel (Phot. 126). If a pan which has remained bare and stable is secondarily drained into a channel, its stagnancy ceases and it is invaded by vegetation, and may be ultimately obliterated.

Natural transitions from salt marsh to land vegetation unaffected by the tides depend upon the nature of the land abutting upon the tidal zone. Where this is a sand dune or shingle complex there is a narrow zone of vegetation occasionally reached by an exceptionally high spring tide and marked by such plants as *Agropyron pungens*, a kind of couch-grass with sharply pointed leaves, stag's-horn plantain (*Plantago coronopus*), the sea lavenders *Limonium reticulatum* and *bellidifolium*, and often some sand-dune plants.

Where there is freshwater from streams entering the marsh there occur a number of freshwater-marsh plants such as species of rush (*Juncus*), common reed (*Phragmites*), lesser spearwort (*Ranunculus flammula*), and various others that can tolerate a certain amount of salt. Characteristic of such places are water dropwort (*Oenanthe lachenalii*) and brookweed (*Samolus valerandi*).

Where grassland borders on the marsh a number of pasture plants begin to come in on the edges, such as the grasses *Hordeum nodosum* (a kind of barley grass), crested dog's-tail (*Cynosurus cristatus*), cocksfoot (*Dactylis glomerata*), and the red and white clovers. Mixed with these are remains of the salt-marsh flora such as thrift, and other plants of the upper marsh.

CHAPTER XVI

MARITIME VEGETATION

(*continued*)

Foreshore and Sand Dunes

ON open sandy seashores undisturbed by human interference a scattered vegetation of flowering plants is often found along the zone—the foreshore—just reached or barely reached by the highest spring tides. This strictly *littoral* vegetation can only maintain itself where it is not too constantly and violently disturbed. The soil must be fairly stable, not subject to constant erosion by wind or waves, and not overwhelmed by sand or shingle. These conditions are often met with at the seaward foot of sand dunes which are not growing very actively nor being eroded by the sea or wind. Of course, such conditions are not maintained indefinitely. Sooner or later a violent storm or an exceptionally high tide, or both together, will destroy the habitat and its plants, which can only re-establish themselves when quiet conditions return.

The foreshore community (Phot. 128) consists mainly of annual plants, scattered and irregularly spaced, and mainly belonging to the families Chenopodiaceae, Cruciferae, and Polygonaceae. Perhaps the two most constant and characteristic species on sandy shores at the foot of sand dunes are the sea rocket (*Cakile maritima*, Phot. 129), with succulent leaves and pretty pink flowers, and the spiny saltwort (*Salsola kali*, Phot. 128). Frequent, too, are species of orache (*Atriplex*), sea knotgrasses (*Polygonum littorale* and *P. raii*), and species of the white-flowered scurvy-grass (*Cochlearia*), some on sandy and some on loamy soils. The sea radish (*Raphanus maritimus*) and the perennial sea beet (*Beta maritima*) also occur in such situations on loamy soils. These foreshore plants, like those of shingle beaches, depend very much on the tidal drift left at high spring-tide mark and consisting largely of dead seaweeds, which contribute humus to the soil. The

soil, of course, contains a large amount of salt from much drenching with sea spray, and the plants of the foreshore communities, like the salt-marsh plants, are halophytes, often with fleshy leaves.

SAND-DUNE VEGETATION

In this country the accumulations of blown sand known as sand dunes are almost confined to the sea coast, though small dune areas are formed inland in a few places, for instance on the sandy tracts of Breckland. By far the greatest and most extensive accumulations of wind-blown sand in the world are the continental dunes of desert, arid, and semi-arid regions, as on the northern edge of the Sahara and in south-west Asia. The essential power which perennial sand-dune plants must possess in order to survive is the capacity to grow up through the sand which is continually blowing over them, and thus their habit and mode of growth is similar whether they inhabit coastal or continental dunes. Unlike salt-marsh plants and the plants of the foreshore communities, most coastal dune plants are not halophytes, though they must tolerate some salt spray. We include the British communities in maritime vegetation, since they occur on the coast, where collectively they cover a considerable area, and are often associated with shingle beaches and salt marshes. They are formed and dominated mainly by marram-grass (*Ammophila arenaria*), which is only found in this habitat, and possess some species like sea spurge, sea holly, sea convolvulus, and horned poppy, which are not found elsewhere except on coastal shingle beaches.

The supply of sand for the formation of coastal dunes comes either from wide, gently sloping sandy flats over which the tide recedes for a long distance so that a great expanse of sand is exposed and dried during the ebb, or from shoals formed offshore and similarly exposed at low tide. The dry grains of sand are driven landward by onshore winds in great quantity, and those which are travelling close to the surface are stopped by any small obstacle, and accumulate round it, both on the windward and especially on the lee side, for there the air is relatively

S. Mangham

PHOT. 128. Foreshore at Holme-next-the-Sea, Norfolk

1. Shingly sand: highest limit of ordinary spring tides
2. Foreshore community: Sea rocket (*Cakile maritima*), saltwort (*Salsola kali*), sea sandwort (*Honckenya*).
3. Foredune of sea couch-grass (*Agropyron junceum*).
4. Main dunes, marram-grass (*Ammophila*) with sea holly.

A. G. T.

PHOT. 129. Sea rocket (*Cakile maritima*) in flower, forming a miniature dune on the foreshore near Camber Castle, East Sussex.

F. W. Oliver

PHOT. 130. Wind-blown marram accumulating sand, Blakeney Far Point, Norfolk.

F. W. Oliver

PHOT. 131. Great Sandy Low, Blakeney Point, holding water left by the last spring tide. In the foreground and between the Low and the sea are young marram dunes. Stabilised dune ridge behind to the left.

quiet and the lighter grains are carried to the top by eddies, coming to rest on the longer and gentler leeward slope. On any fixed obstacle such as a large stone or a lump of stranded seaweed the sand hill so formed can grow no higher than the top of the obstacle: thus a brushwood fence fixed across a sand-laden windway will accumulate sand up to the height of the fence, and no higher. But a growing plant can push its shoots upwards and sideways as it becomes covered with sand, thus constantly extending the obstacle, so that the embryo dune goes on growing in size and height until it is stopped from other causes. It is in this way that large and lofty dune systems are formed by plants which have exceptional powers of pushing their shoots through the sand and continually forming fresh roots in the moist sand which one always finds just below the air-dry surface layer.

If a new series of dunes arises on the seaward side of one which is already established, the latter is more or less protected from the sand-laden wind and ceases to grow in height, so that it may be equalled or overtopped by the new range. In this way several parallel ranges of dunes are often formed. Sand-dune complexes arise on the flat shores of sandy bays facing prevailing winds, on the tops of shingle spits running across estuaries, and in other situations where blowing sand is trapped and colonised by dune-forming plants.

FOREDUNES

Just behind the foreshore community described on p. 239 low dunes are often formed, particularly by the sea couch-grass (*Agropyron junceum*, Phot. 128). This plant is closely allied to the common couch-grass or "twitch" (*A. repens*), which is such a pestilent weed of arable and garden land, and like common twitch it sends out stiff pointed runners which penetrate the surrounding soil and propagate the plant. Sea couch-grass can withstand short immersions in sea water and is thus able to grow within reach of the highest spring tides. Its runners penetrate deeply into sand and even shingle, so that they are not exposed to surface erosion, while the shoots can grow up

through a moderate amount of sand accumulated above. In this way the plant often forms a range of low dunes at or just above the level reached by high spring tides. These "foredunes" never reach any considerable height, for the power of the plant to grow up through superincumbent sand is restricted—3 or 4 feet is a common limit.

Typically the *Agropyron* foredunes are found immediately behind the annuals of the foreshore community (Phot. 128), but the two are often mixed up, the annuals settling between or sometimes even behind the foredunes. An annual plant cannot itself be a regular dune-former, because it has no power of continuing to grow up through sand, but blown sand accumulates, of course, round any plant and thus tiny transient sand hills are produced by such plants as *Cakile* and *Salsola,* whose skeletons may hold the sand through the winter. One plant of this habitat, the perennial sea sandwort, *Honckenya peploides,* since it has a creeping habit, does, however, form temporary foredunes, though of even lesser height than the *Agropyron* dunes (Phot. 132).

THE MAIN DUNES

Marram-grass (*Ammophila arenaria*), which has long narrow leaves, tightly rolled in dry weather, is almost the sole agent in the building of the main dune ranges. It does not tolerate, as sea couch-grass does, immersion in sea water for any but the shortest periods, and thus cannot grow within reach of spring tides, but seedlings establish themselves on sand or sandy shingle just above the uppermost tide marks. On many stretches of sandy shore Agropyretum is absent, and here *Ammophila* forms the foredunes as well as the main ranges (Phots. 130, 131). The underground runners spread by preference in pure loose sand, and, once established in deep sand, the plant has far greater powers of lateral and vertical growth than *Agropyron,* so that it is able to grow up through many feet of superincumbent sand (provided this is not deposited too quickly), constantly forming fresh roots in the moist sand close to the surface. Thus it is exceedingly well fitted to form massive dunes of great height. When a high dune has been partly removed by a violent gale, as

often happens, the exposed face of sand down to the base level, representing a vertical section of the dune, is seen to be penetrated throughout by the rhizomes and roots of marram, mostly dead, but those near the surface still living and active. Another less common dune-forming grass sometimes accompanying *Ammophila* is the sea lyme-grass (*Elymus arenarius*, Phot. 133).

The marram-grass community is never closed on the surface, the dominant forming separate tufts of long upstanding leaves which are bent right over to leeward during a gale (Phot. 130) with bare sand between. Where the marram tufts are close enough to protect the sand from removal by wind, these interspaces are colonised by a few, mainly non-maritime, species, of which perhaps the commonest is ragwort (*Senecio jacobaea*); others are a kind of hawkweed, *Hieracium umbellatum*, and the two thistles, spear thistle (*Cirsium lanceolatum*) and field thistle (*C. arvense*). The maritime sea holly (*Eryngium maritimum*), with its grey spiny leaves, is also commonly found (Phot. 128).

Though *Ammophila* is practically the sole agent in forming the main dunes, it does little to consolidate the *surface* sand, the wind often removing sand from between the widely spaced tufts of marram, so that unless the rate of supply is at least equal to that of removal, the dune will be eroded, as frequently happens. The first grass to associate itself with the marram is the sand fescue (*Festuca rubra* var. *arenaria*), and this may succeed in consolidating the surface sand. Several other species play a similar part by means of their creeping rhizomes: the sand sedge (*Carex arenaria*), which throws up rosettes of leaves along the line of growth of its rhizome; the sea convolvulus (*Convolvulus soldanella*), with rather fleshy leaves and beautiful pink funnel-shaped flowers; and the two sea spurges, the common species, *Euphorbia paralias*, and the rarer *E. portlandica*, confined to south-western dunes. Other plants, not peculiar to dunes, such as creeping buttercup (*Ranunculus repens*) and silverweed (*Potentilla anserina*), fix small extents of sand on some dunes.

The physiognomy of the main mobile dune complex, with its steeply rolling, highly irregular crests and valleys,

is very characteristic. Stretches of perfectly bare shifting sand on the wind-swept slopes and in the hollows alternate with clumps and tufts of marram which occupy most of the crests. This trackless confusion of crests and hollows is due to the complex distribution of wind currents and eddies, as the streams of quickly moving air are deflected and broken up by the slopes and crests. Throughout the maze of elevations and depressions the same types of surface form are constantly repeated, following the laws of motion of the wind-driven sand, and partially fixed here and there by the marram-grass. The mobile dunes are often called "white" or "yellow dunes" according to the colour of the fresh sand, in contrast to the fixed "grey dunes" dominated by lichens of the genus *Cladonia.*

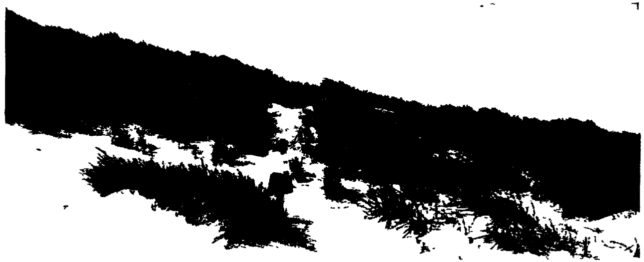
Besides the species of flowering plants mentioned above, which are fairly constant and characteristic, many other non-maritime species may be found in the Ammophiletum of various dune complexes, and the miscellaneous floras of different areas may have very few plants in common. This depends largely on the chance carriage of windborne seed from a distance. Weeds of arable land may be strongly represented. A condition of the colonisation of most of these plants is, no doubt, the occurrence of considerable periods of damp weather when the surface of the sand is moist and fairly stable, since their seeds could not germinate in dry powdery sand. They are all fluctuating and inconstant, liable to be destroyed by erosion or overwhelmed by fresh sand, since few have any power of coping with these occurrences, to which the Ammophiletum is always exposed.

FIXED DUNES

Where the sand becomes partially stabilised by plants like the red fescue that have colonised the Ammophiletum, or where it is protected to some extent from the violence of sea winds, as on the inner side of a range of high dunes, the sand is colonised by mosses, of which the most important are four: *Tortula ruraliformis* (almost confined to sand dunes), *Brachythecium albicans*, *Ceratodon purpureus*, and *Bryum* (several species). These may already have settled in protected areas of the Ammophiletum, and they play

R. H. Compton

Phot. 132. Sea sandwort (*Honckenya*) forming miniature dunes on the foreshore: sparse marram. Holme-next-the-Sea



A. G. T.

Phot. 133. Foredunes with marram (left) and sea-lyme-grass (right). Main dune range behind.

A. G. T.

Phot. 134. Sea buckthorn scrub at back of main dune ridge. Hemsby, Norfolk.

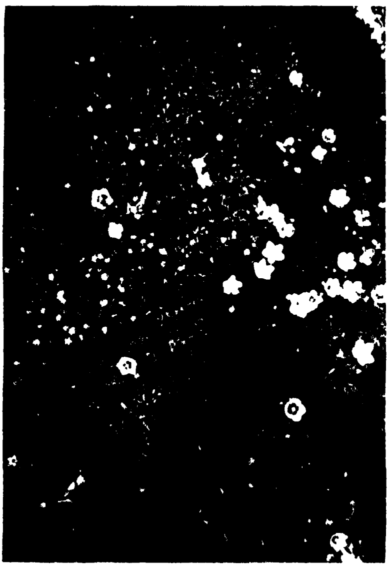
A. G. T.

Phot. 135. Detail of Phot. 134. Sea buckthorn (*Hippophaë*), right; polypody fern, centre; marram, left, etc.

Face p. 244

R. J. Lythgoe

PHOT. 136. Moss carpet of fixed calcareous dune with relict marram, sea holly (*Eryngium maritimum*), smooth hawkbit (*Leontodon nudicaulis*), etc. Castle Gregory, Co. Kerry.



J. Massart

PHOT. 137. Vegetation of a wet "slack," near Southport, Lancs. Grass-of-Parnassus (*Parnassia palustris*), bog pimpernel (*Anagallis tenella*), etc.

the leading part in the transition to fixed dunes. Young thalli[1] of various lichens then appear among the moss shoots, mainly species of *Cladonia, Parmelia, Peltigera,* and *Evernia prunastri,* and the lichens increase so that in the typical "grey dunes" they come to surpass the mosses both in number of individuals and of species, covering the sand with an almost continuous grey carpet.

The fixed dunes are eventually colonised by a large number of flowering plants, with a predominance, in old fixed dunes, of heath and dry grassland species. A certain number of maritime and submaritime species occur, for example thrift, sand sedge, stag's-horn plantain, sea campion. Marram-grass is usually still present, but only in sparse tufts (Phot. 186), with many dead leaves and a generally dingy and moribund appearance. The conditions no longer suit it, perhaps because of the less free aeration of the sand, because of competition with other plants, or because of some toxic effect of the lichen and moss carpet upon its growth. Eventually it dies out altogether.

Photograph 186 shows a typical fixed dune with a carpet of mosses, tufts of moribund marram, and many species of flowering plants, among which a plant of sea holly, and flowers of the hairy hawkbit (*Leontodon nudicaulis*) and of a pink centaury (*Centaurium littorale*) are conspicuous.

At this stage of the succession the plant carpet loses its "maritime" character, and its further development depends upon the particular conditions. Where the sand is highly calcareous ("white dunes"), composed of minute shells, comminuted fragments of larger shells, or of corals and nullipores, many calcicolous species appear and, under grazing, the fixed dune becomes a calcareous pasture with a flora practically identical with grassland on chalk or limestone. If the sand is mainly of quartz grains, usually tinged with ferric salts ("yellow dunes"), heath tends to develop, grass heath if it is grazed or heavily infested with rabbits, ling or scrub heath if it is left alone. On the east coast of England the sea buckthorn (*Hippophaë rhamnoides*), with scaly grey leaves, forms a scrub in some places (Phots. 184, 185). In this country the shrub occurs wild only on

[1] The word *thallus* is applied to the vegetative body of a lower plant not differentiated into stem and leaf.

coastal dunes, though on the Continent it grows on shingle and gravel by the side of streams. Dune scrub is, however, usually formed by the commoner inland shrubs, largely thorny species like gorse, blackthorn, bramble, and rose: elder is also common. All of these are more or less resistant to rabbit attack. The pretty burnet rose, densely covered with thorns (*Rosa spinosissima*), is very frequent on some calcareous dunes.

Natural woodland is not formed on our coastal dunes—partly, no doubt, because of their relatively small extent and the constant human interference with the vegetation of fixed dunes; largely also because of the prevailing scarcity of seed parents, which is particularly marked in coastal regions. Planted pines, especially the Austrian pine (*Pinus nigra* var. *austriaca*), but also Scots and Corsican pines, do very well in sufficiently protected places, and may be used to help fix dune areas. There are extensive pine plantations on the dunes of part of the Norfolk coast and on the Culbin Sands in eastern Scotland.

Low-lying areas among the dunes where water is held up by an impermeable stratum of heavy soil below the sand are often marshy, or even hold pools of fresh or sometimes brackish water, depending on whether the water comes from rain or freshwater springs alone, or whether the tide gets occasional access. Such depressions are commonly known as "slacks." They are much more frequent in our west coast dunes where the climate is damp.

Standing pools in the slacks may contain a few fresh or brackish water plants, and the marshy edges often support quite a good marsh flora which does not differ from that of an inland marsh, including species of sedge and rush, marsh pennywort (*Hydrocotyle*), water mint, etc., and also aquatic mosses and algae. A striking species which is found in this habitat is grass-of-Parnassus (*Parnassia palustris*), with conspicuous white flowers and beautifully veined petals (Phot. 187), elsewhere common on boggy ground in hilly regions of the north and west. A few salt-marsh species such as sea rush (*Juncus maritimus*), sea pimpernel (*Glaux maritima*), and submaritimes (see p. 257) such as brookweed (*Samolus valerandi*) and *Scirpus holoschoenus*, a very rare west coast species, may also occur.

On certain west coasts, e.g. the Ainsdale dunes of Lancashire (and also on the north coasts of France and Belgium), a variety of the creeping willow (*Salix repens*) may colonise the marshy slacks, its seeds germinating in the wet soil. If the quantity of blown sand falling in the slack is slight, the creeping willow maintains itself at about the original level and the accompanying flora is that of a dune marsh; but if more sand is supplied, the shoots of the willow grow up through it, above the ground water level, and a drier habitat is established, with abundant humus from the dead willow leaves. In this we may find characteristic humus plants such as the saprophytic [1] "bird's nest" (*Monotropa hypopitys*) which we saw (p. 102) as a characteristic species of beechwood humus, and species of wintergreen (*Pirola*) which grow mainly in northern and western woods and on heaths rich in humus.

When the sand supply is still more abundant most of the species are suppressed, but the creeping willow continues to grow up through the sand, putting out fresh roots just below the surface, and thus forms quite big dunes on the site of an old slack, rivalling in height those formed by marram-grass, and with a flora scarcely differing from that of ordinary mobile dunes.

A characteristic feature of sand-dune complexes is the formation of the so-called "blow-outs." Unusually violent wind, especially in an unusual direction, may blow away the whole side of a partly fixed dune, exposing the interior with its skeleton of old marram stems and roots, and often excavating a great hole in the sand. Such a "blow-out" may persist for a long time, but is eventually gradually revegetated if no fresh disturbance takes place.

Fixed-dune areas are sometimes used for rough grazing of sheep or even cattle, but they are not capable of supporting much stock. Very often they are devoted to rabbit-warren, since the rabbits find the easily excavated, though fairly coherent, sand of fixed dunes extremely suitable for making their burrows. The constant scratching of rabbits on a fixed-dune ridge destroys the carpet of vegetation in particular places, laying the sand bare and

[1] Depending on organic substances derived from humus.

so giving the wind a purchase and leading to the formation of a "blow-out."

Sand-dune areas are traditionally used as golf links, for which they are ideal. The fairway is formed largely over the smooth fixed dunes, the putting greens are sown with special grass seed mixtures and kept carefully mown and rolled, while the irregular contours of the semi-mobile marram dunes provide any desired abundance of bunkers and hazards.

CHAPTER XVII

MARITIME VEGETATION

(*continued*)

Shingle Beaches : Submaritime Habitats

SHINGLE beaches are composed of water-worn pebbles of very various size; they are originally derived by erosion from sea cliffs of hard rocks or from flints embedded in the chalk, and dislodged as the chalk cliffs are worn back by the sea. Driven along the coast by currents and worn down to rounded form by constant attrition, they are thrown up by the incoming tide to form banks of shingle on certain stretches of low-lying shore. In this way the simplest type of shingle beach—the *fringing beach* familiar along much of our south coast—is formed.

Not only is submerged shingle moved along the sea bottom but the pebble beaches and spits themselves gradually travel along the coast through the action of obliquely directed waves coming from the direction of prevailing winds. These throw up shingle at an angle with the line of the beach, and on the ebbing of each wave some of the pebbles travel back down the beach at right angles to its axis so that they come to rest further along the beach. In this way a constant lateral movement of the shingle is maintained. This drift along the coast is evidenced by the almost complete removal of the shingle from certain beaches which sometimes occurs, and is checked by the construction of "groynes" at right angles to the shore line. On the south coast the drift is from west to east, as can be seen by the frequent piling up of shingle on the western sides of the groynes. On the coast of east Norfolk and Suffolk the drift is from north to south, of north Norfolk from east to west.

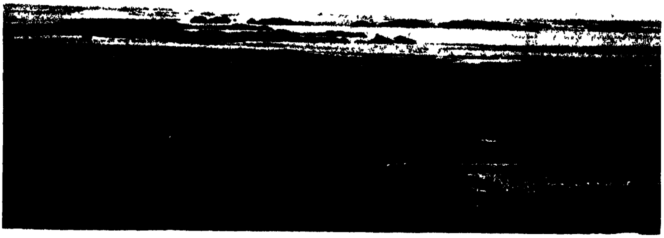
These directions of drift are also seen in the formation of *shingle spits.* When the line of the coast changes direction, falling away landwards at the mouth of a bay or estuary, the shingle is often carried on in a direct line

with the fringing beach, leaving the shore and forming a bank or spit projecting into the sea across the bay or estuary, whose mouth is thus deflected. On the south coast these spits are directed eastward, on the east coast southward, on the north coast of Norfolk westward. Some shingle spits are several miles long; the longest is Orford beach on the Suffolk coast, which extends southward for 12 miles from its base at Aldeburgh, crossing the mouths of the Alde and Butley rivers, whose waters can only escape to the open sea far to the south of their original points of exit.

Shingle spits are usually gently curved inwards towards their extremities, and the free tip itself is commonly sharply bent towards the land, forming a *hook*. Such hooks are repeatedly formed during the growth of the spit in periods of violent storms when the growing tip of the main spit is driven landwards. In the quieter years between the stormy phases the growth of the main spit is continued in the original direction, so that successive hooks come to form lateral appendages of the main bank, directed towards the land. In this way quite complex shingle systems are sometimes formed, and upon them sand dunes are often built up, while on the comparatively quiet tidal ground on the landward side of the spit salt marsh is usually developed, separate marshes being often formed in the concavities of the successive "hooks."

Sometimes a shingle spit may stretch right across a bay, joining the shore again on the opposite side, and it is then called a *shingle bar*. The famous Chesil beach in Dorset is such a bar for much of its length, and may have been originally formed as a spit. It is the longest of all our continuous shingle beaches, with a total length of 18 miles.

A fourth type of shingle beach has been called an *apposition beach*. This is formed when successive banks of pebbles are laid down side by side so as to produce a wide expanse of shingle, the landward parts of which are removed altogether from the sea (Phot. 188). The most extensive of these tracts of shingle is at Dungeness, and there is a smaller one at Pevensey. Where the individual banks can be distinguished they are called *shingle fulls*. A wide shingle spit may show apposition of parallel shingle



A. G. T.

PHOT. 138. General view of the great apposition shingle beach west of the River Rother, near Rye, Sussex. Shingle "fulls" (ridges) covered with grass used as sheep pasture in the foreground. Beyond is largely bare shingle with patches of scrub.

A. G. T.

PHOT. 139. Shingle fulls with sea campion (*Silene maritima*) and the characteristic dock (*Rumex crispus* var. *trigranulatus*). The "lows" between the fulls are uncolonised. Orford Beach, Suffolk.

A. G. T.

PHOT. 140. Maritime variety of herb-robert (*Geranium robertianum*) at the back of the tidal beach near Rye, E. Sussex.

F. W. Oliver

Phot. 141. Looking north-west along the Fleet, a lagoon between Chesil Beach (left) and the mainland. "Deltas" of shingle project into the Fleet beyond the belt of shrubby sea blite (*Suaeda fruticosa*). Back of the beach with sea campion on the left behind.

F. W. Oliver

[illegible] feeding on sea campion on Chesil Beach where it is a fringing beach near Burton Bradstock. The sheep had come down from the mainland at the end of a long drought when their usual pastures were dried up. The plants on the shingle were still fresh. *September 1911.*

Face p. 2[illegible]1

fulls, as can be seen in the Orford beach (Phot. 189). The vegetation of the landward parts of such a beach is non-maritime, consisting of scrub or grass, and is comparable with that of an old fixed dune.

The shingle spit is the most interesting form of shingle beach, because it shows all phases of development and the greatest variety of vegetation. Definite regions are recognisable on the surface of a cross-section of a shingle spit or bar. On the seaward side there is often a succession of "steps" corresponding with the levels reached by tides of different heights. The highest of these is usually well marked, and is known as the *storm shelf*—the highest level to which shingle is carried by the highest spring tides when backed by a strong wind. The actual summit or *crest* of the beach only receives shingle when there is an exceptionally high spring tide backed by an onshore gale. In these conditions shingle is often carried right over and down the *back* of the beach, which slopes gently to the inner edge.

The shingle of our coastal beaches is sometimes almost pure, but usually mixed with sand in various proportions. Sand and shingle are both constantly thrown up by the sea and carried on to a shingle beach, but much of the sand is again washed back by retreating waves. Thus the shingle of the storm shelf is normally nearly pure, but other parts of the beach usually contain mixtures of sand and shingle in various proportions.

The humus content of a young shingle beach, like that of a foredune, is derived entirely from the disintegration of tidal drift, but after the beach is occupied by vegetation it is, of course, added to by the decayed remains of the beach plants. The presence of finely divided humus between the stones can easily be verified by delving into the beach with the fingers, which are quickly soiled by contact with the dark humus material. It is, of course, the mixture of sand and humus on which the plants depend for their nutrition, since the stones themselves cannot provide it.

The water content of a shingle beach is considerable. In the hottest summers and on the hottest days water is found within a few inches of the surface. This water is usually fresh and quite drinkable, containing very little salt except close to the edge of the sea and, in the case of a spit pro-

tecting a salt marsh behind it, close to the edge of the salt marsh. It is no doubt derived mainly from rain, but dew formation, both on the surface of the beach and by condensation on the surface of stones some distance down, may make a considerable contribution. Shingle plants never suffer from drought. This is strikingly illustrated by Photograph 142, which shows sheep coming on to the Chesil beach to graze on sea campion when their usual land pastures were dried up at the end of a long drought.

There are no dominants of shingle beaches in the sense in which marram-grass dominates mobile sand dunes. The flora is rather poor in species except on the summits of old "hooks" where the maritime element has almost disappeared and the vegetation, like that of old fixed dunes, consists of inland plants. But a few species are very characteristic of shingle, and of these several are also found on dunes. There has been little comparative work on the vegetation of different shingle beaches, and the following account is mainly based on the shingle of Blakeney Point on the north coast of Norfolk, which has been most closely studied. It certainly applies in many respects, however, to other shingle beaches.

A common plant on the Blakeney beach is the sea sandwort (*Honckenya peploides*), which we have already seen as a foredune species (Phot. 132), and which colonises shingle beaches where the sand fraction is considerable. It approaches the sea more closely than most shingle plants, sometimes occurring on the crest of the beach. The leaves are somewhat succulent, but it is not quite a complete halophyte, since prolonged immersion in sea water turns its leaves yellow. A very important and abundant shingle plant is the sea campion (*Silene maritima*, Phots. 139, 142), which is not infrequent on partly fixed dunes but is even more characteristic of shingle beaches. Both these species are able to endure covering by stones as well as by sand, and with their deep roots and abundant aerial shoots they form extensive carpets on the beach and contribute considerably to its stabilisation.

The horned poppy with large yellow flowers (*Glaucium flavum*), so called from the long curved pods, and a variety

of the curly dock (*Rumex crispus* var. *trigranulatus*, Phot. 139), unlike the last two, are erect, comparatively tall plants and are conspicuous on all the less sterile portions on the back of the beach, where the high tides coming over the salt marshes bring abundant drift for the making of humus and also the seeds which renew the population. These four species are all strictly maritime plants, and all (except perhaps *Honckenya*) more often found on shingle beaches than on sand dunes.

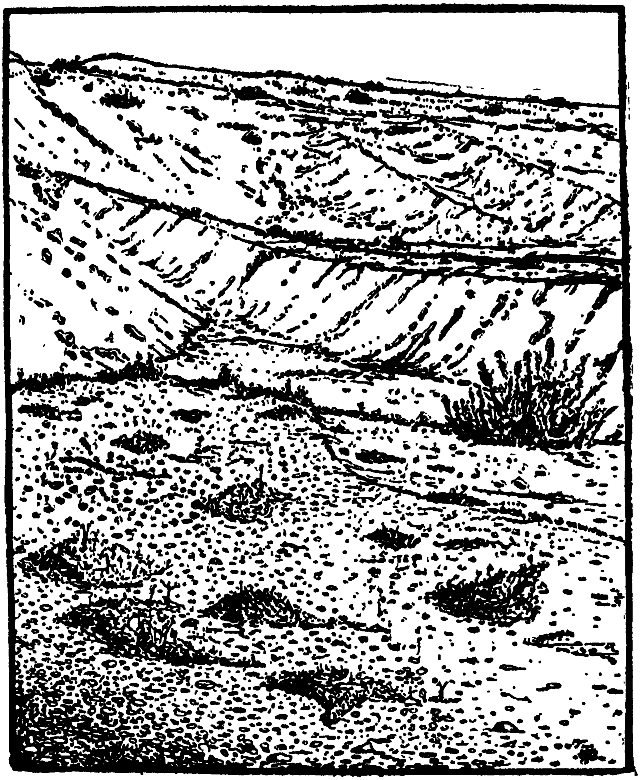
Three other characteristic shingle-beach plants (not found on Blakeney Point) are the purple herb-robert (*Geranium purpureum*), which has a general resemblance to the common herb-robert, but with more narrowly cut, rather succulent leaves, while the whole plant is tinged with purple: this is found on the shingle of south-western coasts;[1] the sea vetchling or sea pea (*Lathyrus maritimus*), with purple flowers fading to blue, a very local plant of east and south coast shingle beaches, though at one time very abundant at certain places and still so on the Chesil and Orford beaches; and the sea nightshade (*Solanum dulcamara* var. *marinum*), prostrate and with fleshy leaves, on the south coast shingle.

A very remarkable plant found on the edges of some of our east and south coast beaches where these abut on salt marsh is the shrubby sea blite (*Suaeda fruticosa*). This has already been referred to as a salt-marsh plant (p. 235), but it rarely occurs and is never luxuriant except where the salt-marsh soil in which it is rooted is covered with shingle. On the Blakeney beach tidal drift coming up the estuary and over the salt marshes is deposited in great quantity by the spring tides on the inner edge of the main shingle bank and on the lateral banks where these abut on the salt marsh. This drift contains abundant ripe seeds of *Suaeda* and here they germinate in great numbers, so that the bushes come to line the shingle banks in continuous belts, spreading over the flat crests of the lower laterals which are covered by the high spring tides. They cannot establish themselves, however, on those parts of the inner

[1] Phot. 140 shows a variety of the common herb-robert from a Kentish shingle beach very much like *G. purpureum* which is said not to occur so far east.

edge of the main bank where there is much wave action. Belts and isolated clumps of *Suaeda* also occur higher up the back of the bank as far as the crest. These are plants which originally germinated on the inner edge of the bank when this was situated farther seaward. As the whole shingle bank gradually travels landwards by the impact of the waves dislodging the shingle and carrying it over the crest during violent storms coinciding with high spring tides, the *Suaeda* plants on the inner edge of the beach are covered with shingle thrown over the crest and down the back of the beach, but are able to grow up through it so as to maintain their leafy shoots above the surface. In fact, the plants show increased luxuriance after a period of this pounding and covering with stones. In this way the *Suaeda* can "climb" the back of the bank as far as the crest. What actually happens is a progressive shifting of the whole bank across the line occupied by the plants, which was originally the inner edge of the bank where the seeds germinated and the plants started their growth. The lower parts of the woody stems, deeply buried in shingle, of those plants which have thus "climbed" the beach eventually die and disintegrate, the younger shoots rooting afresh between the stones of the surface shingle. This added luxuriance of shingle-covered plants is shown too by the sea sandwort (*Honckenya*) and by the sea campion (*Silene maritima*), which are also often covered by fresh shingle in their habitats on the crest and back of the beach. The parallel with the behaviour of marram on mobile sand dunes (p. 240) is obvious.

On the inner margin of the great Chesil Bank in Dorset *Suaeda fruticosa* forms a continuous belt on the low terrace of shingle at the edge of the "Fleet"—the lagoon separating the beach from the mainland (Phot. 141). Here, however, the conditions are different and the plants show no tendency to climb the bank, since there is no continuous shifting of surface shingle over the site of the bushes. The inward travel of shingle on the landward side of the Chesil is confined to certain spots where water is forced through the lofty beach and gushes out on the landward side above the Fleet, dislodging the shingle and excavating narrow ravines, locally called "cans" (Fig. 8). At the outlet of



T. G. Hill.

FIG. 8. Sketch of the back of Chesil Beach from the shingle terrace near the margin of the Fleet, showing the ravines or "cans" down which shingle is dislodged by sea-water forced through the beach. A bush of shrubby sea blite (*Suaeda fruticosa*) is seen on the terrace with scattered plants of sea campion (*Silene maritima*), as also on the flat tops of the ridges left between the cans and on the back of the beach behind.

each "can" shingle is carried forward into the Fleet, forming a small "delta" (Phot. 141). There is no tidal drift in the almost stagnant Fleet, and therefore no germination of freshly arrived *Suaeda* seeds.

Besides the characteristic shingle plants described above, a number of other species occur on shingle beaches. The storm shelf at Blakeney is mostly bare of vegetation, though there is an occasional plant of sea beet (*Beta maritima*) or a prostrate orache (*Atriplex*), and on the crest itself the vegetation is also very sparse. Both these habitats are

fully exposed to wind and wave action at high spring tides and frequently drenched with spray. But on the back of the beach and near the edge of the salt marsh many plants occur in addition to those already mentioned. Of these there are half a dozen species which are at home in the middle and upper salt marsh, and as many sand-dune plants. A species of "twitch" with sharp pointed leaves (*Agropyron pungens*) is a characteristic plant of the zone just reached by the highest spring tides on the banks above the marsh. Of non-maritime plants, the red fescue (*Festuca rubra*) usually occurs between the ranks of *Suaeda* bushes on the sheltered side, and with two kinds of sow thistle (*Sonchus*) is characteristic of the most stable shingle where there is abundant tidal drift. Patches of yellow stonecrop (*Sedum acre*) are also common in these places. Several other grasses, including the ubiquitous annual meadow-grass (*Poa annua*), are more or less common where they can find enough soil, and so is the common groundsel (*Senecio vulgaris*).

The stable lateral shingle banks at Blakeney Point, which have been formed in the past from successive landward deflections of the tip of the growing main bank (formation of "hooks," see p. 250), show various stages of the development of land vegetation, and on each there is a regular zoning of communities from the edge of the salt marsh to the crest of the bank. This succession culminates in the "high elbow" of some of the banks at the beginning of the L-shaped termination of the original "hook." Here there is an abundance of thrift (*Armeria maritima*), but nearly all the other plants are non-maritime, belonging largely to light inland soils.

On the great expanses of "apposition shingle," as at Dungeness on the borders of Kent and Sussex, there is a much more extensive development of land vegetation, for which there is no opportunity in a system of narrow shingle spits like those at Blakeney Point. Here the shingle, now relatively remote from the sea, supports not only a variety of grasses and ruderal plants but also scrub of gorse, bramble, blackthorn, hawthorn, and elder, corresponding with the much greater development of soil, besides the removal from maritime influences (Phot. 188).

SUBMARITIME HABITATS

Finally, we must briefly consider the vegetation of habitats more or less subject to maritime influences but not belonging to the well-marked maritime plant formations described in the last chapters.

First of all there are the coastal rocks and cliffs above the reach of the tide but constantly exposed to sea spray. Here we find definitely halophytic species, most of them salt-marsh species, such as sea plantain, sea lavender, and thrift, but some which do not occur in salt marshes and must have a well-aerated soil. Prominent among them is the samphire (*Crithmum maritimum*), an umbelliferous plant with compound leaves divided into long, very fleshy segments. Other plants which are almost confined to such situations are the beet (*Beta maritima*)—which, however, also occurs on the foreshore and on shingle beaches—and the much less common wild cabbage (*Brassica oleracea*), both plants with large, expanded leaves, the ancestors of familiar garden vegetables, and found wild on our southern and south-western coasts. Then there is fennel (*Foeniculum vulgare*), a tall plant with finely divided leaves, and queen stock (*Matthiola incana*), also confined to some spots on the south coast. The tree mallow (*Lavatera arborea*), a shrub with large handsome pink flowers, is found on some maritime rocks.

Cliff slopes and ledges bear a great mixture of vegetation. First there are the fragments of communities which occupy the ground on the tops of the cliffs, usually grassland or moorland. Then there are "fissure plants" (*chasmophytes*) growing in rock clefts—often woodland (shade) species; sometimes lichens on bare rock faces; and finally the halophytes already mentioned and inland plants which are tolerant of salt in places especially exposed to sea spray. The whole flora is, of course, influenced by the nature of the rock and the soil, whether it is calcareous or not, and whether much or little humus is formed.

The grazing factor is nearly always important in these cliff communities. Sheep grazing on the tops of the cliffs constantly reach seemingly inaccessible ledges, eating the turf short and often leaving other traces of their presence.

The difference made by their absence is well seen on certain actually inaccessible islets, which are covered by dense growths of tall grasses, particularly the red fescue, in spite of extreme exposure to wind and spray.

A common plant community on the steep islands and headlands of the west coast of Ireland, the soil constantly soaked with spray in winter gales and also grazed by sheep or rabbits or both, has been called a "plantain sward." Of very low growth—often not more than half an inch high—and with the plants forming tiny rosettes of leaves, it is dominated by the sea plantain (*Plantago maritima*), usually in company with stag's-horn plantain (*P. coronopus*), and sometimes the common ribwort (*P. lanceolata*). In some of these swards the flora is quite rich, including a considerable variety of grasses and grassland herbs; but in extreme cases the plantains form by far the greater bulk of the vegetation and mere scraps of other species are present, while occasionally there are no plants present except the plantains.

Other submaritime habitats are the brackish ditches and marshes which often adjoin estuaries and are common behind the shingle beaches of our south coast. To these the tide has no direct access, but they are occasionally invaded by sea water, and because of poor drainage remain brackish indefinitely. Such marshes have often been formerly "reclaimed" from salt marsh and partially drained by ditches, but owing to defective sluices or the difficulty of adequate drainage the water has remained brackish and the land practically derelict.

Brackish ditches are inhabited by some characteristic water plants, many of which can also grow in completely fresh water. Such are a kind of water crowfoot, *Ranunculus baudotii*, some of the pondweeds, e.g. *Potamogeton pectinatus* and *P. filiformis*; and the allied plants, of very similar habit, with linear or filiform leaves and very small flowers, *Ruppia maritima* and *Zannichellia palustris*. Various green algae, too, such as species of *Vaucheria*, also grow in these ditches.

A number of tall reedswamp plants belonging to the sedge family are found in or on the edges of the brackish ditches—species of *Scirpus* (*S. maritimus*, *S. tabernae-*

montani) and *Carex*, and the handsome "flowering rush" (*Butomus umbellatus*) with tall umbels of rose-coloured flowers, which also grows in freshwater ditches. Marsh mallow (*Althaea officinalis*), with large conspicuous pink flowers, is another plant of brackish marshes.

Quite a number of plants which are by no means confined to the coast are nevertheless more abundant as we approach the sea. Among these are the wild carrot (*Daucus carota*), the common storksbill (*Erodium cicutarium*) and more markedly the musk storksbill (*E. moschatum*), a species of thistle (*Carduus tenuiflorus*) with numerous small crowded heads of pale purple flowers, one of the mouse-ear chick-weeds, *Cerastium tetrandrum*, and alexanders (*Smyrnium olusatrum*). The causes of this peculiar submaritime distribution are not understood.

CHAPTER XVIII

THE FUTURE OF THE GREEN MANTLE[1]

We have now surveyed the varied natural and partly natural plant communities which (if we include the enclosed permanent grass) cover more than half the land surface of Great Britain. The purely artificial vegetation—the arable crops and the plantations of exotic trees—have not been considered: their nature, and the problems they raise, are different, and belong particularly to the sphere of agriculture and forestry, though much that can be learned from the study of semi-natural grassland and native woods is of value in these domains of applied science. The principles of ecology are valid for any community of plants, because they depend on the reactions of the organism to its condition of existence—climate and soil and the effects of accompanying plants and animals—as well as on the nature of the changes which active vegetation brings about in the soil in which it grows. A general description of British crops and plantations, that part of the Green Mantle which we have directly created for our own use and put in the place of the natural vegetation which once occupied the ground, would be of great value and ought to be undertaken, but it lies outside the scope of this book. We can, however, consider the changes which are likely to occur in what is left of the natural Green Mantle.

Apart from the extension of building and other public and industrial works which directly destroy vegetation, there are two main activities which concern us most intimately. The first is the change from "permanent" grassland to ploughland, the other the planting of trees on heath, moorland, and rough grazings, and the substitution of coniferous plantations for native deciduous woodland.

During the late war a great deal of permanent grass was

[1] Most of the topics considered in this chapter are dealt with more fully in my book *Our Heritage of Wild Nature* (Cambridge University Press, 1945. Price 8s. 6d.).

ploughed up and arable crops sown (see pp. 1-2), resulting in a very considerable increase in home food production. Primarily there was a great extension of the acreage under such typical crops as wheat and potatoes, which was most marked, amounting to an increase of several times the pre-war area in the midland and western counties of England which formerly had a great preponderance of permanent grass. There was also, in the later years of the war, a very considerable increase in temporary grass or ley. This, of course, also involved ploughing, and if we take ordinary arable crops and leys together, they increased during the war from 36 per cent. to 60 per cent. of the farm area of England and Wales.

During the lean years ahead of us we shall certainly keep a greatly increased means of food production at home, and not only for the extra wheat and potatoes and sugar but also for the superior stock-feeding value of the leys as compared with the former great extent of inferior permanent pasture. More extensive ley farming, consistently advocated by Sir George Stapledon, has come to stay, and it gives the opportunity of sowing the greatly improved strains of pasture grasses and clovers, many of which were bred by Stapledon's staff during the years when he was Director of the Bureau of Plant Breeding at Aberystwyth.

The great diminution of permanent grass resulting from this wide new ploughing is almost an unmixed good, and we certainly need not regret the disappearance of so much of the semi-natural permanent grassland, often uninteresting and dreary, besides being of very little agricultural value. Here and there, no doubt, interesting plants have been destroyed, but the total natural history loss is certainly more than balanced by the agricultural gain. Some of the best permanent pastures, for example the famous Leicestershire grasslands, on which bullocks could be fattened without recourse to extraneous feeding, have been preserved.

Stapledon, however, wants to see "improved" many of the hillside "rough grazings" as well as the enclosed "permanent grass." Some of his most striking experiments were carried out on areas such as Cahn Hill near

Aberystwyth, where hill grassland which had never been sown was ploughed, manured, and sown with pedigree grasses, resulting in an immense increase in its grazing value. Such treatment, of course, considerably alters the character of the flora, but it does not radically change the nature of the landscape. Grass-covered hills remain grass-covered hills, though the kinds of grass growing on them and the accompanying plants are different. Some considerable areas of the old rough grazings, with their vegetation which has come by itself, should not be interfered with, for they are a well-marked type of British semi-natural vegetation and contain many interesting plants. There would be little justification for a scheme of resowing the whole of our rough grazings, at least until all the enclosed pastures had been made to give their maximum yield; and indeed there is little likelihood of any such scheme being implemented because of their enormous extent.

A much more serious threat comes from the Forestry Commission, which desires to plant altogether one-fifth of the whole existing area of rough grazings (three million acres). Tree planting, of course, does completely change the character of the landscape, replacing the open commons and hillsides by thick tree-growth, destroying the existing vegetation and depriving the walker of the free air and distant views which make up the unique attraction of our hill regions. Up to now the Commission has been rather starved of money and has had to buy cheap land wherever it was available and suitable for planting. The result has been that in many places it has cut into sheep-raising (rough-grazing) areas and upset their economy by depriving them of certain areas which formed essential parts of the framework of sheep farming. If the proportion of the whole country under forest is to be largely increased, as has now been decided, it would seem better that the areas devoted to planting (especially of conifers), should be more concentrated, all available land (with certain exceptions to be mentioned later) being planted in some regions and the existing use of others left undisturbed.

In addition to hill grassland the Forestry Commission have planted extensive areas of heath and moorland—heath

especially in Dorset and the Breckland, moorland in Wales, the north of England, and Scotland. Such land is of very much less value than the hill grassland for purposes other than forestry, though some of it is grazed and peat-cutting is practised on some of the deeper peat soils. This is, of course, apart from the use of very large tracts of upland heath and moorland for grouse-preserving and for deer-stalking—purposes legitimate in themselves, but concerned with the enjoyment of too small sections of the population to justify the setting apart of so great a proportion of our hill and mountain country for such enjoyment alone. Not all the moorland is plantable. Much of it is too boggy and much lies at too high an altitude. And some of the moorland scenery should be kept for its beauty, for the enjoyment of the walker, and because it is clothed with characteristic plant communities.

Besides planting on open hill grassland and moorland, the Forestry Commission have replanted many of our deciduous woods with conifers, and it is proposed to take over the planting and supervision of two million acres of private woodland. In order to justify itself economically the Commission have had to plant mainly conifers, the current demand for "softwood" representing, they say, 96 per cent. of the total demand; and this policy will undoubtedly be continued.

The massive planting of conifers profoundly alters the whole character of the landscape. Open country is covered with a thick blanket of trees, and the specific beauty of broad-leaved deciduous woodland is replaced by the dreary uniformity of the evergreen canopy. This is especially marked when, as is the common practice, an even-aged plantation of conifers is felled before the trees are mature, in response to a market demand. Young coniferous plantations, straight-edged and neat in form, with precisely aligned saplings, are not beautiful objects. When a coniferous (or any other) woodland can be allowed to grow to maturity with progressive thinning, and then selectively felled, some trees being left to supply seed for natural regeneration, the case is quite different. But for this, of course, the trees have to be perfectly suited to the particular climate and soil. Anyone who compares the

ugly formal spruce plantations of southern Sweden, where the natural woods are of oak and beech, with the lovely natural spruce forests of central and north-central Sweden, with their trees of all ages and irregular heathy undergrowth, will appreciate the difference.

The result of planting or replanting with conifers is to destroy the plants of open grassland or heathland or the original undergrowth of a deciduous woodland and most of the animals which lived in it. This is partly the result of the deep shade cast by most conifers, and partly because of the effect on the soil of the accumulation of the fallen needles, which tends to convert the mild humus or mull of the deciduous forest floor into raw humus or mor (see p. 36). The floor of a young conifer plantation is often completely bare of plants. A few may survive and continue to live in the plantation, and other species sometimes come in, but any undergrowth there may be is in no way comparable for richness and beauty with the original flora.

All this applies primarily to the clay and loam soils of the English lowlands, a natural region of deciduous forest, mainly oak forest. Many of the old oakwoods are now practically derelict, so far as providing marketable timber is concerned, owing to centuries of neglect and misuse, and a report of the Forestry Commission (1943) remarks that "the large areas of second and third class oak of moderate and small dimensions have not justified their existence." This is certainly true, but we cannot immediately conclude that they ought all to be destroyed and replanted with conifers. Many of them could be rehabilitated by proper management. After all, England is a country in which oak was at one time dominant and produced good enough timber.

In the hill country of the north and north-west the picture is entirely different. Here we have very poorly wooded regions in which deciduous trees, apart from birch, do not flourish except in sheltered valleys. It is a natural climate of coniferous forest which is now represented only by fragments of pinewood, because the last phases of the Ice Age and the subsequent insulation of Britain prevented the re-immigration of spruce (native here in pre-glacial times) and the creation of forests like those of Scandinavia.

The north European forests themselves, however, are very poor in species, unlike those of the north-west of North America, which has a great wealth of magnificent conifers. It is this source to which we must mainly look to supplement the European poverty. Douglas fir (*Pseudotsuga mucronata*) and Sitka spruce (*Picea sitchensis*) are two of the leading dominants of that region, and together with the "western cedar" (*Thuja plicata*) the Forestry Commission have already used them extensively in their new plantations.

What we should like to see is the creation of great new permanent coniferous forests of whatever species are found to flourish, to grow to maturity, and to set viable seed in these regions, and not even-aged plantations destined to be clear-felled, scattered throughout the country, unbeautiful in themselves, quite out of harmony with the landscape and destructive of our native flora and fauna.

The timber from such forests should produce an ample supply of softwood, and their exploitation by selective felling would not interfere with their beauty and interest. There are plenty of examples on the Continent. In the lowlands and on many of the lower hillsides the existing oakwoods should be preserved and rehabilitated by proper management and where necessary by replanting. The wholesale felling that the demands of two wars have made necessary certainly renders extensive planting essential. Mixed planting of hardwoods and conifers is often advocated, and there is a good deal to be said for it on various grounds, but as many woods as possible of our native deciduous trees—oak, ash, and beech—should be perpetuated on the soils on which they naturally grow. On the lowland heaths on sandy soil conifers are more in place than on the clays and loams. The Forestry Commission have already planted extensive woods of this kind in several heath regions, and there is no reason why other heaths should not be similarly planted. But some of our heaths should be preserved as heaths.

The beechwoods of the chalk downs have a particular and very high claim to preservation, for their special loveliness and for their characteristic plants and animals. Some of them are still exploited for their very useful timber

on the selective system which preserves them as permanent beautiful woods, and it is to be hoped that this practice may be extended. It is understood that the Forestry Commission does intend to make beech a permanent crop on suitable soils. Most of the chalk escarpments are still, however, grassland, as they have been through the centuries, and the preservation of much of these as grassland is most desirable on grounds both of public enjoyment and ecological interest. Conifer plantations on the chalk should be avoided as far as possible.

In these ways we can maintain the beauty and interest of our Green Mantle, modifying its character here and there in accordance with modern needs, but preserving most of its essential historic character. It would be unreasonable and ridiculous to ignore legitimate economic demands, but it is none the less essential to take other values—of beauty, sentiment, and scientific interest—into full consideration. If we do not, we shall bequeath to our descendants a defaced and ugly land.

The modern movement to establish National Parks and Nature Reserves can contribute in an important degree to the preservation of the Green Mantle. In the National Parks, which will extend over wide areas for the public enjoyment of beautiful landscape, the existing uses of the land will be in no way interfered with, but destructive "development" will be prevented, and in "Conservation Areas" of typical pieces of still rural country it is proposed to maintain existing conditions as far as possible. National Nature Reserves will be smaller areas, chosen as characteristic samples of natural and semi-natural vegetation with the animals which inhabit it; and their primary object will be to preserve such samples for scientific study, though the reserves will be open to the public under appropriate regulations wherever there is no danger of defeating the essential purpose for which they were selected. In many cases they will also serve as centres of education in natural history.

It is also proposed to establish a "Biological Service," concerned with the continuous investigation of the wild life of the country, both plants and animals, so that it may be more effectively conserved and controlled through

increased understanding of the nature and requirements of its varied constituents—the plant and animal communities and species.

It is hoped that these proposals may be implemented in the near future, and if they develop satisfactorily they should, taken together, do much to ensure the continued maintenance of our precious and incomparable natural heritage of wild nature.

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